TRUE *STROPHOMENA* AND A REVISION OF THE CLASSIFICATION AND EVOLUTION OF STROPHOMENOID AND 'STROPHODONTOID' BRACHIOPODS

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ABSTRACT. The brachiopod superfamily Strophomenoidea is reviewed and reclassified, with chief emphasis on the form and evolution of the cardinalia, the denticulation, the ventral muscle fields, and the dorsal side septa. There are six families without denticulation along the hinge line: the Christianiidae, Foliomenidae, Glyptomenidae, Leptaenoideidae, Rafinesquinidae, and Strophomenidae; and seven families with denticles along the hinge line: the Amphistrophiidae, Douvillinidae, Eopholidostrophiidae, Leptostrophiidae, Shaleriidae, Strophodontidae and Strophonellidae. A separate superfamily 'Strophodontacea' is not recognized since denticulation arose polyphyletically, mainly from different stocks within the Rafinesquinidae. Experimentation in the development of denticles and crenulations in the Strophomenidae, Leptaeninae and other groups also occurred but was unsuccessful. The form of the cardinalia is the most important character for differentiating families apart from the later denticulate genera, in which parallel evolution of the cardinalia occurred, and the form of the ventral valve muscle field and other structures are used. A lectotype is selected for *Strophomena planumbona*, the type species of *Strophomena*, and the new genus *Palaeoleptostrophia* is erected, with type species *Stropheodonta jamesoni*, from the lower Llandovery (Rhuddanian) of Girvan, Scotland. *Brachyprion*, *Eostropheodonta*, *Leptaena*, *Rhenostrophia*, and associated genera are revised, and the new family Eopholidostrophiidae is erected.

WHILST undertaking synoptic work for the revised brachiopod volume of the *Treatise on invertebrate paleontology*, we realized that the classification of the strophomenoid genera within subfamilies, families and superfamilies required fundamental revision. The group includes the key genera *Strophomena* and *Leptaena*, which at the time of their erection in the early nineteenth century were thought to encompass a wide range of brachiopods. Thus for example, in Davidson's great monograph on the fossil brachiopods of Britain (1871, pls 39–49), the illustrations of '*Strophomena*' figured forms now included in *Amphistrophia*, *Brachyprion*, *Christiania*, *Colaptomena*, *Coolinia*, *Dactylogonia*, *Eostropheodonta*, *Eostrophonella*, *Gunnarella*, *Isophragma*, *Katastrophomena*, *Kiaeromena*, *Lepidoleptaena*, *Leptaena*, *Leptostrophia*, *Mackerrovia*, *Macrocoelia*, *Megastrophia*, *Mesopholidostrophia*, *Morinorhynchus*, *Oepikina*, *Pentlandina*, *Ptychoglyptus*, *Rafinesquina*, *Shaleria*, *Strophomena*, and *Strophonella*; and the illustrations of '*Leptaena*' include brachiopods now assigned to *Bimuria*, *Christiania*, *Eoplectodonta*, *Kjaerina*, *Leangella*, *Mesopholidostrophia*, *Shagamella*, *Sowerbyella*, and *Sowerbyites* (Cocks 1978). What has happened since is that key groups, such as the Plectambonitoidea (including *Bimuria*, *Eoplectodonta*, *Isophragma*, *Leangella*, *Ptychoglyptus*, *Sowerbyella*, and *Sowerbyites* in the above list), with their distinctive simple, trifid or undercut cardinal processes as opposed to the bifid cardinal processes of the Strophomenoidea, have been separated from the main strophomenoid concept. Similarly, the chonetoids (including *Shagamella* above), with their spines along the ventral cardinal margin, have long been recognized as a separate suborder, as have also the orthotetoids, with their impunctate shells in Ordovician and Silurian forms (including *Morinorhynchus* and *Coolinia*).

Thus the reduced, but nevertheless abundant and important group, requires reclassification. In

the past this has been done chiefly by grouping shell shapes and profiles together, with, for example the resupinate Strophomenidae, the convexo-concave Rafinesquinidae and the rugose Leptaenidae, but, as discussed below, these characters we consider to represent merely generic, rather than familial, differences. Today there are about two hundred and fifty nominal genera within the group, although we consider many to be subjective synonyms; nevertheless their logical allocation to appropriate groups of familial or greater or lesser rank, is one of the tasks that form the core of this paper. The other is to investigate the acquisition of denticles along the hinge line and thus to assess the true relationship between the strophomenoids and the 'strophodontoids'. After assessment of all the available characters, the morphology and the evolution of the cardinalia and of the denticulation have been found to be the two most important criteria. In this paper we use the term 'strophodontoid' to include all strophomenoids with denticles on the hinge line; however, this does not imply that we recognize the Strophodontoidea as a separate superfamily (see below).

HISTORY OF FAMILIAL CLASSIFICATION

From 1846, when King erected the Strophomenidae, attention has been caught by this conspicuous group of Palaeozoic brachiopods. In the nineteenth century the Strophomenidae were separated from the spiny chonetoids and productoids by the absence of external spines. In 1893 Schuchert distinguished the Rafinesquininae as a subfamily of the Strophomenidae on the basis of shell outline and profile, but this was published at the time that Hall and Clarke (1894) was in press, otherwise the latter would have been unlikely to have persisted with the erection of the Leptaenidae. In the present century, Jones (1928) separated the plectambonitoids on the basis of shell shape as a subfamily within the Strophomenidae, and Caster (1939) erected the subfamily Stropheodontinae (with the tribes Stropheodontini, Douvillinini and Leptostrophiini) and also the subfamily Strophonellinae for strophomenoids with denticles on their hinge lines; Stainbrook (1943) erected the Pholidostrophiinae within the latter. However, the first review with anything like a rational basis of division for the strophomenoids as a whole was that by Williams (1953b), who followed Öpik's earlier studies in recognizing the fundamental importance of the difference between the simple or trifid cardinal processes of the plectambonitoids and the bifid cardinal processes of the other groups and elevated the Strophomenacea, Plectambonitacea, and Orthotetacea to superfamilial rank. Williams recognized the importance of a cemented mode of life by erecting the Liljevalliinae and Leptaenoideinae as subfamilies and also distinguished the very individual Christianiidae as a family for the first time. Together with the Oepikininae previously erected by Sokolskaya (1960) and the Foliomenidae, Furcitellinae, Glyptomeninae, Leptodontellinae, and the Shaleriidae, all erected in the volume, this formed the classification used in Williams (1965). Shortly afterwards, Havlíček (1967) proposed the Eostropheodontidae and Elliptostrophiidae, together with numerous new genera, in his substantial monograph on the Strophomenida from Czechoslovakia and Harper (1973) erected the Amphistrophiinae. In 1976 Pope reviewed the Strophomenacea and erected a new subfamily Murinellidae and the tribe Teratelasmini within a new classification based on a complicated mixture of the perceived type of pseudopunctae, the overall shape, the dental lamellae and teeth, and, at a lower level the form of the cardinal process and other interior and exterior features.

Sokolskaya (1960) had been the first to treat the forms with internal hinge denticles as a superfamily Stropheodontacea, separate from the superfamily Strophomenacea, and this was followed by various authors, but not by Williams (e.g. 1965), Cocks (1967, 1968) or Bassett (1971). Cocks (1978, p. 124) regarded the acquisition of denticles as polyphyletic and thus did not regard the Stropheodontacea as a valid monophyletic superfamily. Harper and Boucot (1978) reviewed what they termed the Stropheodontacea at length, with many new genera and nine new families and subfamilies, namely the Brachyprioninae, Douvillinellinae, Lissostrophiidae, Mesodouvillininae, Mesoleptostrophiinae, Nervostrophiinae, Protodouvillininae, Teichostrophiinae, and Telaeoshaleri-idae. Since that time there has been a relative pause in activity, with only the family Maoristrophiidae

Ushatinskaya and Alekseeva (1983) and the subfamilies Megastrophiinae Jahnke (1981) and Dicoelostrophiinae Wang and Rong (1986) added to the list of over thirty available taxa of familial and subfamilial rank within the strophomenoids (not including the plectambonitoids and orthotetoids).

## KEY MORPHOLOGICAL CHARACTERS

Cardinalia types

We have recognized four different types of cardinalia within the strophomenoids with smooth hinge lines, termed A to D on Text-figure 1 and the key to the terminology on Text-figure 2. The three chief differences
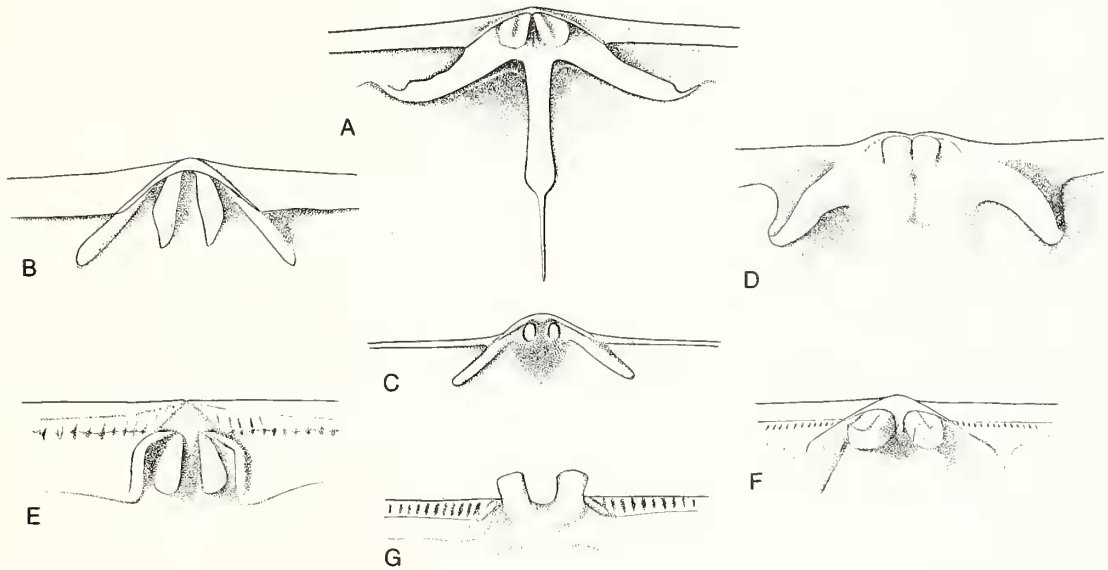

TEXT-FIG. 1. The seven types of strophomenoid cardinalia. Type A, based on *Strophomena*; Type B, based on *Kjerulfina*; Type C, based on *Bystromena*; Type D, based on *Christiania*; Type E, based on *Leptostrophia*; Type F, based on *Amphistrophia*; Type G, based on *Strophodonta*.

are (a) the general shape of the cardinal process lobes, (b) their position relative to the hinge line and socket ridges, and (c) the attitude of the socket ridges and their relationship to the cardinal process lobes. The four types are (A) the *Strophomena* type (Pl. 1, fig. 7; Text-fig. 1A), which have robust and often oval cardinal process lobes situated on the posterior part of a notothyrial platform which is usually prominent. The process lobes can be discrete, but are sometimes fused together at the bases before merging with the notothyrial platform, as in *Oepikina* (Pl. 3, fig. 7). The cardinal process lobes are situated either upon the hinge line, or slightly postero-ventrally to it, and do not project anteriorly to any large degree. In addition, in many genera the socket ridges are curved posterolaterally – a feature not seen in any other cardinalia type. Type B is shown by *Kjerulfina* (Text-fig. 1B) and *Kjaerina* (Pl. 3, figs 1–5), in which the cardinal process lobes are elongate or plate-like in shape and remain entirely discrete throughout ontogeny. Most of the lobes are situated anterior to the hinge line, extending even as far as the anterior ends of the socket ridges. The notothyrial platform is variably developed; sometimes, e.g. *Kjerulfina*, it is absent and in other genera, such as in some species of *Kjaerina* (Pl. 3, fig. 2) and *Rafinesquina* (Pl. 2, fig. 5), it is well developed. The socket ridges are straight and usually smaller than in Type A, and were more important in the early growth stages of some genera; for example, in *Leptaena rugosa* the smaller specimens (Pl. 4, fig. 4; Text-fig. 4) have more prominent socket ridges
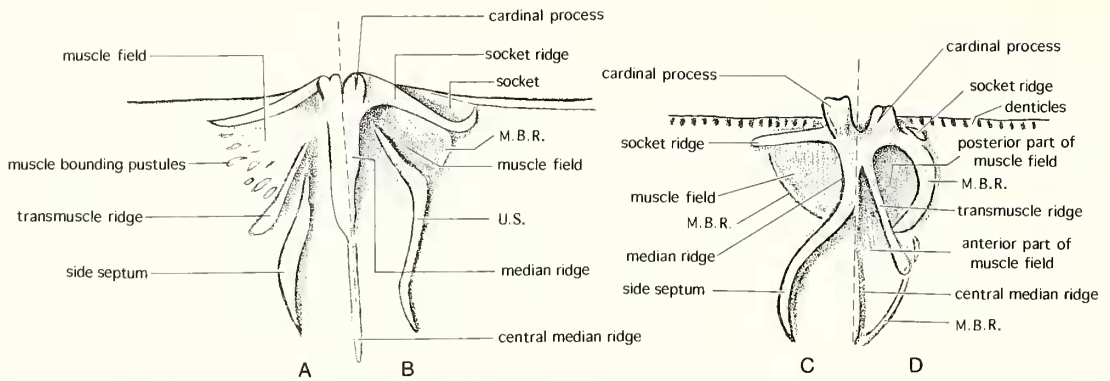
TEXT-FIG. 2. Strophomenoid dorsal valve morphology, showing the terminology used here. A, *Dactylogonia*; B, *Quondongia*; C, *Protodouvillina*; D, *Malurostrophia*. M.B.R., muscle bounding ridge; U.S., united structure of transmuscle ridge and side septum.
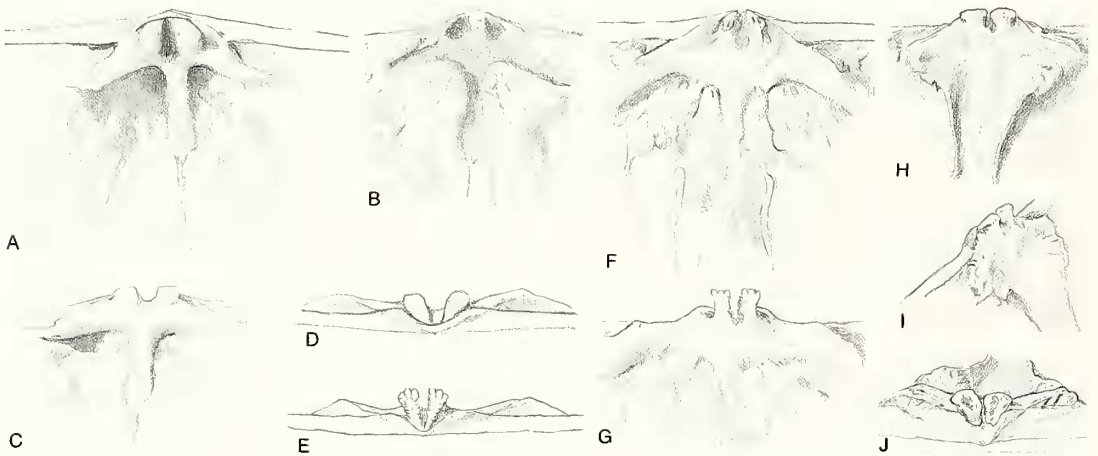
TEXT-FIG. 3. Cardinalia typical of the family Strophomenidae. A–D, *Strophomena planumbona*, based on AMNH 918/5. E–G, *Murinella partita* Cooper, based on USNM 117640. H–J, *Biparetis paucirugosus* Amsden, based on OGS 6716; all × 3.

than the gerontic individuals (Pl. 4, fig. 2). In a few extreme genera, for example *Rafinesquina* itself, the cardinal process lobes are extremely strong and ponderous and dwarf the socket ridges in size (Pl. 2, figs 1–7; Text-fig. 2). The cardinalia of Type C are delicate, such as those in *Paromalomena* and *Bystromena* (Text-figs 1c, 6), with small cardinal process lobes on or largely posterior to the hinge line. The socket ridges are directly fused in some cases to the bases of cardinal process lobes. There is usually no notothyrial platform. There is often a concave area immediately anterior to the cardinal process lobes. Type D has only been found in *Christiania* (= *Christianella* Liang) (Text-figs 1D, 7), in which the low cardinal process lobes are very close together and fused at their bases. The socket plates (note the use of the term 'plate' here rather than 'ridge' to emphasize their strength) are often elevated from the valve floor anteriorly.

There are three additional types of cardinalia in the 'strophodontoids', which we term E, F and G. However, many early stocks, such as *Eostrophonella* (Pl. 5, fig. 4), *Palaeoleptostrophia* gen. nov. (Pl. 4, fig. 8) and *Eostropheodonta* in the Ashgill and Llandovery, have Type B cardinalia. Type E is characterized by strong,

TEXT-FIG. 4. The cardinalia of a medium-size specimen of topotype *Leptaena rugosa*. A, internal mould. B–E, various views of latex cast; all based on BB 67946; ×6.

thick, plate-like cardinal process lobes directed ventrally and which are not developed posteriorly beyond the cardinal margin, such as in *Leptostrophia* (Pl. 7, fig. 6; Text-fig. 7). Socket ridges may be present but they are usually small and situated close to or postero-lateral to the cardinal process lobes, as in *Leptostrophia*, or absent, as in *Protoleptostrophia*. The cardinal process lobes are variably divergent and are sometimes even convergent onto a median ridge, as in *Mesoleptostrophia filosa* (Text-fig. 20). In Type F the cardinal process lobes are relatively small but swollen and knob-like and they are ventrally (not posteriorly) directed, as in *Amphistrophia striata* (Text-fig. 1F) and *Shaleria* (*Janiomya*) *ornatella* (Text-fig. 19). This type is seen mainly in later Silurian amphistrophiids and shaleriids, but has not been recorded in leptostrophiids. In Type G the cardinal process lobes are strong and posteriorly directed, as in *Strophodonta* itself (Pl. 7, fig. 5; Text-fig. 1G),
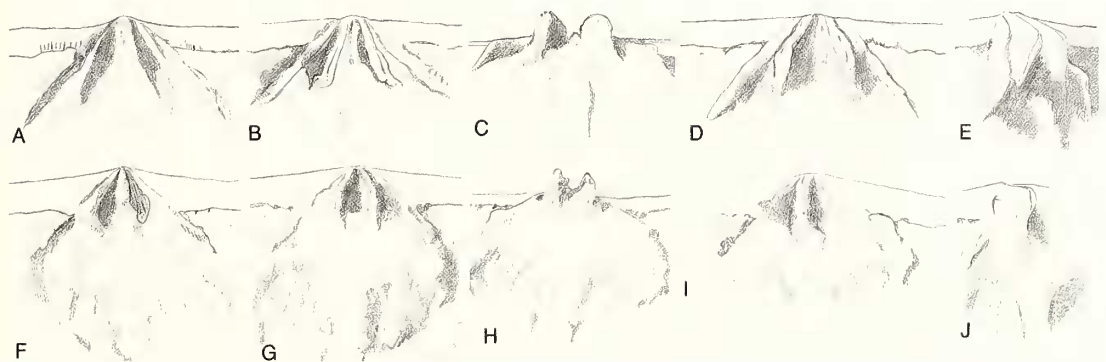
TEXT-FIG. 5. Cardinalia of A–E, *Eostrophonella eothen* based on BC 50617, compared with, F–J, *Kjerulfina polycyma* based on BB 73901; all ×6. In both series the chilidium is not shown.

and their bases may or may not be united. Type G is seen mainly in Devonian strophodontids and douvillinids, but seldom in leptostrophiids. Socket ridges are usually developed, but they are often short and even absent in *Pholidostrophia* and *Lissostrophia*. Type F was probably the ancestor of Type G and was probably derived in turn from Type B. Type E may also have been derived from Type B.

Teeth, denticles, and crenulations

Most early brachiopods, particularly orthoids, have a simple articulation consisting of a pair of teeth in the ventral valve which interlocked with a pair of sockets in the dorsal valve. The sockets are negative features formed between the hinge at their posterior edge and a pair of plates or ridges, termed socket plates or socket ridges, at their anterior edge. Many early strophomenoids had this simple configuration of teeth and sockets. In contrast, some more advanced 'strophodontoids' had replaced the simple tooth and socket system by a number of denticles, which were spread along part or all of the hinge line of both valves to provide additional

articulation. These denticles appeared for the first time in the latest Ordovician (Ashgill) in genera such as *Origostrophia* Mitchell, 1977.

However, between these two extreme forms of articulation there are a number of structures present in various strophomenoid genera whose function is difficult to interpret in detail, but whose general purpose was probably to make the articulation system more efficient. These structures take the form of a variety of regular or irregular striae found on various facets of the teeth and socket ridges, and also on anterior extensions of the hinge line, some of which form composite structures with the teeth. Various terminologies have been used to describe these structures and the striae occurring on them, for example Williams (1951, fig. 22) showed *Eostropheodonta* as possessing composite structures including dental plates and denticular plates, both of which carried what he termed denticles. However, in this paper we reserve the use of 'denticles' to include striae on the hinge lines only, or on anterior extensions in the same plane as, or just below, the hinge; the striae on the interior-facing teeth or socket ridges we term 'crenulations'. A particular variation arises when two different types of striae are seen on adjacent facets of the teeth, for example in *Biparetis* (Text-figs 8, 13), in which only the antero-median crenulations on the teeth intermesh with similar crenulations on the socket ridges; the finer striations on the posterior part have no counterparts in the dorsal valve. Striations may be regular, as in *Biparetis*, or irregular, as in *Strophomena* itself (Pl. 1, fig. 10), where striations bifurcate or
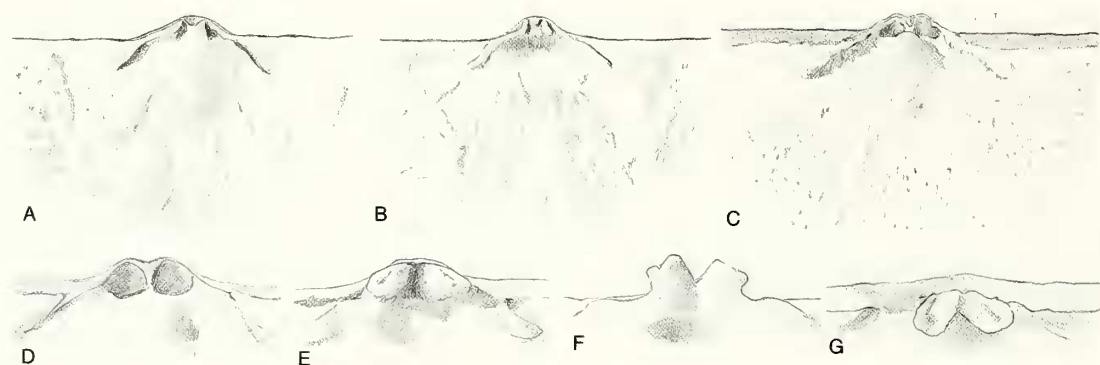

TEXT-FIG. 6. Cardinalia of Type C. A–B, *Bystromena perplexa* based on BB 35367; ×6. C–G, *Paromalomena polonica*; C, based on BB 29666 and D–G, on BB 29216; ×12.

coalesce and are often also sinuous. All 'strophodontoid' denticles are essentially regular, and we only attribute the term 'strophodontoid' to those strophomenoids with denticles on the hinge line. Crenulations and striations on the teeth and the sockets are common in many taxa of strophomenoids and have been observed by many authors (such as Spjeldnaes 1957, p. 20; Amsden 1974, p. 52; Pope 1976, p. 192; Harper and Boucot 1978; Harper *et al.* 1985, p. 300) although the developmental degree of these structures is different and in many genera they are absent. However, this has not created much attention. For example, *Eostropheodonta* and *Aphanomena*, both of which have crenulations and denticles (Text-fig. 8), have been ascribed to several different families – the Leptostrophiidae by Williams (1965), Eostropheodontidae by Havlíček (1967) and Rafinesquinidae by Bergström (1968). Even the species name *strophodontoides* has been questionably assigned to the genus *Rafinesquina* itself (Amsden 1974), although we attribute this taxon to *Eostropheodonta*.

Similar crenulations can be seen in several families, not all of which are closely related, and they are found in the strophomenoids listed in the Appendix. There can be great variation within a single population, and crenulations (although not strophodontoid denticles) can be present, feebly developed or absent; for example, in *Katastrophomena woodlandensis* we have observed different individuals both with and without crenulations in the dorsal valves (Text-fig. 11).

Dorsal internal ridges and septa

In other brachiopod groups, the term 'septum' is used for a substantial internal structure, usually at right angles to the valve floor. Since most strophomenoids have relatively little space between the two valves, the term septum is used for much less substantial structures. Indeed there is no real difference in practice between
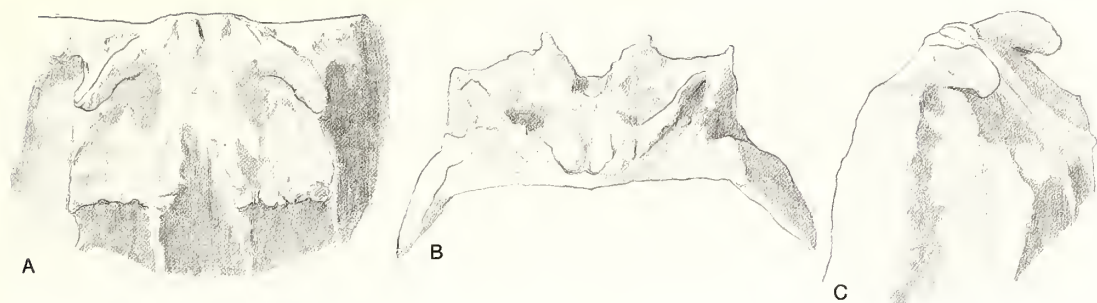
TEXT-FIG. 7. Cardinalia of Type D, as seen in *Christiania subquadrata*, based on BB 11931; from the Lenoir Formation of Tennessee; × 12.

the use of 'septum' and the use of 'ridge', except that the latter can also embrace even smaller structures. We only use the term septum (plural septa) for relatively substantial structures, for example the septa in *Christiania* (Text-fig. 7). There is much variation in septal strength, for example within dorsal valves of *Katastrophomena woodlandensis* the paired side septa can be present or absent in specimens of the same size within the same population and even when present they are of variable strength (Cocks 1968). We use the term 'side septa' in the same way as in the Plectambonitoidea (Cocks and Rong 1989) and include the submedian septa of Williams (1962) and Havlíček (1967), the brachial ridges and brace plates of Harper *et al.* (1967) and Harper and Boucot (1978) and the lateral septa of Zhang (1989). Sometimes the side septa are 1, united with lateral muscle bounding ridges as in *Laevicyphomena*, *Hingganoleptaena* and the 'winglike plates' of *Biparetis* (Text-fig. 3), 2, united with trans-muscle ridges as in *Maakina*, *Oepikina* and *Teratelasma*, and 3, separated from trans-muscle ridges as in *Bekkerina*. The term 'trans-muscle septa' is used for the pair or pairs of septa which diverge anterolaterally as if from a point posteriorly on the median plane of the valve (e.g. in *Oepikina*, Pl. 3, figs 6–7). These trans-muscle septa can also be developed very variably within a single population (Cocks 1968) such as in *Katastrophomena woodlandensis*; however, they are a conservative feature in other stocks.

Other dorsal valve structures

Within the plectambonitoid ancestors of the Strophomenoidea there are two fundamentally different elevated structures with rims running subparallel to the valve margin, the bema and the platform (Cocks and Rong 1989). The bema originates at or near the anterior ends of the socket ridges, whilst the platform originates near to the posterolateral margins of the shell. The bema served as an adductor muscle attachment platform, whilst the raised border of the platform functioned as a barrier to prevent sediment from reaching the lophophore. Some plectambonitoids such as *Leangella* have both bema and platform, although the platform is sometimes developed only in fully mature individuals. The bema is known in strophomenoids (with the possible exception of *Christiania* (Text-fig. 7), but the platform is variably present, even in some of the earliest strophomenoids such as '*Macrocoelia*' *llandeiloensis elongata* of Llanvirn age (Lockley and Williams 1981). The platform is variably developed, usually close to the anterolateral margin of the shell, sometimes in the middle between the bema and the shell margin, and rarely close to the muscle field. In addition there is an internal build-up of secondary shell at the geniculation point of some strophomenoids, particularly *Leptaena*, and we use the term subperipheral rim (= the apophragma of Kelly 1967, p. 591, text-fig. 1). Subperipheral rims can also occur in the ventral valve, but they are relatively uncommon.

Ventral muscle fields and other structures

Dental plates support the teeth and run between the latter and the valve floor. Most strophomenoids possess dental plates, but upon the acquisition of 'strophodontoid' denticles most stocks lack teeth and dental plates, although some early denticulate forms retained them (Williams 1953*a*, fig. 4), and there are sporadic occurrences into the Devonian. The reason for their lack in most 'strophodontoids' is that the strong denticular articulation made their retention unnecessary. There are three basic types of ventral valve interior in strophomenoids lacking hinge line denticles.
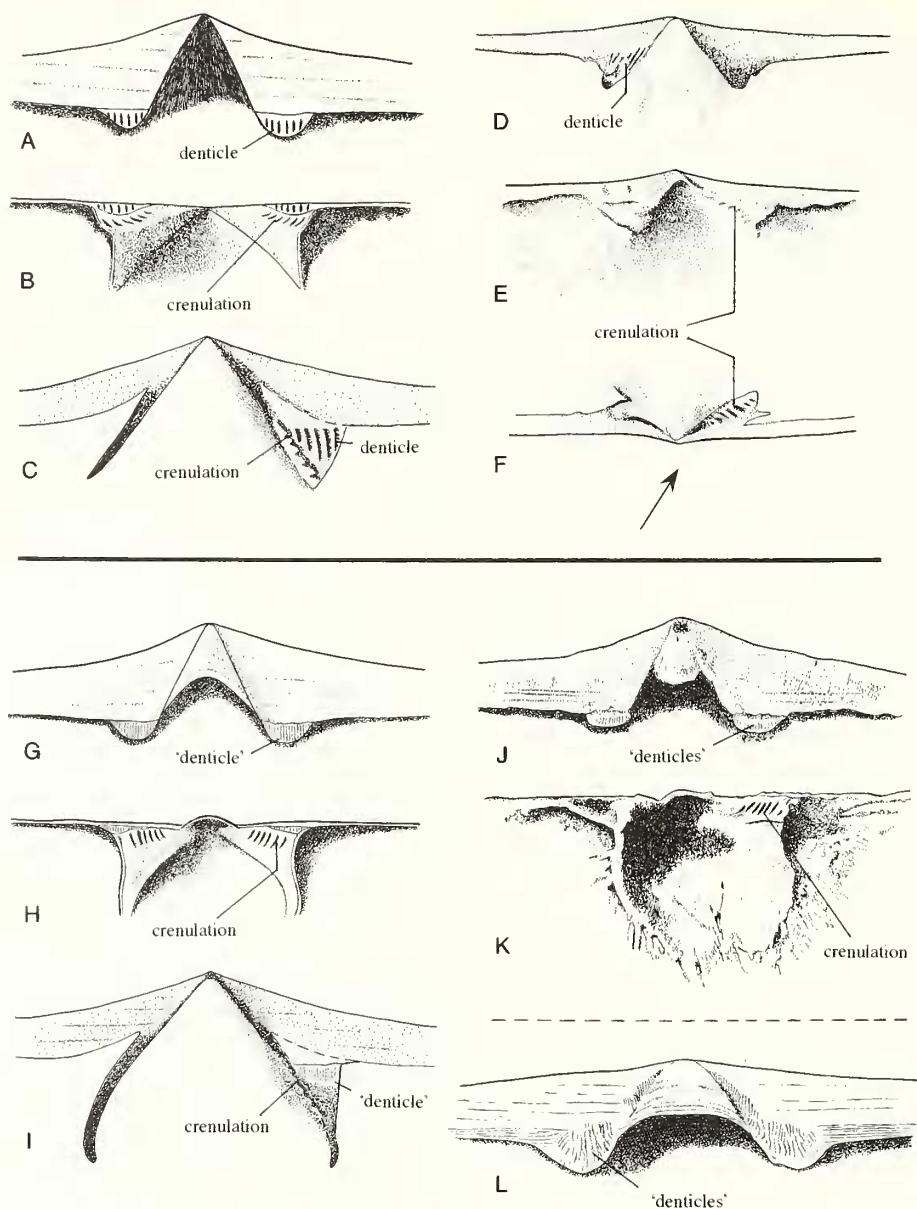
TEXT-FIG. 8. The development of denticles. A–F were successful in acquiring denticles and G–L were unsuccessful. A–C, *Eostropheodonta*. A, ventro posterior view of the ventral interarea with open delthyrium and denticulate teeth; B, anterior view of the dental plates with denticles on the top of the teeth and crenulations on the antero-median facets; C, internal mould of ventral valve showing dental plates, denticles and crenulations. D–F, *Eostropheodonta hirnantensis* based on BB 29257. D, internal mould of ventral valve showing dental plates and denticles; E, latex cast of ventral internal mould showing dental plates and crenulations; F, posterior view of ventral internal mould showing dental plates and crenulations: G–I, *Biparetis*. G, ventro posterior view of the ventral interarea with a covered delthyrium and irregular and many finely denticulated teeth; H, anterior view of the dental plates with 'denticles' and crenulations which do not correspond on the antero median facets of the teeth; I, internal mould of ventral valve showing dental plates, irregular and very fine 'denticles' and crenulations. J–K, *Biparetis paucirugosus* based on Oklahoma University 6703; J, ventroposterior view of the

Type A, exemplified by both *Strophomena* and *Leptaena*, has strong teeth and dental plates, and muscle bounding ridges that are usually fused to the anterior ends of the dental plates. These muscle bounding ridges curve round, either to merge anteriorly with the valve floor, or to coalesce anteriorly. There is a wide variety of shape in the muscle bounding ridges, which are sometimes so massive as to be raised well clear of the valve floor. There is often a myophragm (a median ridge between the pairs of muscles) developed, which does not usually start at the valve apex.

Type B, exemplified by *Rainfesquina*, also has dental plates, but these are usually short and straight. Muscle bounding ridges are usually absent or weak, but if they are present are relatively straight antero-lateral extensions of the ends of the dental plates.

The third type has a bilobed muscle field and vascular markings anterior to it, reminiscent of such plectambonitoids as *Leangella* and *Aegiria*. This Type C has a muscle field which is smaller in relation to the entire valve size than Types A and B, and is typified by both *Christiania* and *Foliomena*. Type C can be subdivided into two kinds, C1, with no dental plates, as in *Foliomena*, and C2 sometimes with well-developed dental plates (Williams 1962, pl. 19, fig. 6), although sometimes the dental plates are only visible as stout ridges under the teeth, as in *Christiania* (Cooper 1956, pl. 214, figs 22–24). In C1 there are no bounding ridges, and the muscle field is weakly impressed and usually has a faint border to the field in which a ridge-like myophragm is well developed (Havlíček 1967; Sheehan 1973). In C2, the border of the two diductor scars is often relatively clear since they are bounded laterally by a pair of thin parallel or slightly divergent dental plates. The anterior ends of the two diductor scars are continuous with a pair of vascula media. Six basic patterns of ventral and dorsal muscle fields were recognized by Williams (1953a) within the 'strophodontoids'. They are douvillinid, leptostrophiid, megastrophiid, shaleriid, strophodontid, and strophonellid muscle scars. Since the muscle fields of strophodontids and megastrophiids are not fundamentally different, we do not use the term megastrophiid muscle scars. We add the mesodouvillinid type (Text-fig. 9c) as a common shape of muscle scar. There are also (a) some different kinds of bilobate ventral muscle scars (e.g. Text-fig. 9 g–h) and (b) very weak scars without any bounding ridges, as in *Eostropheodonta* (Text-fig. 9a) and *Eopholidostrophia*.

Valve profile and ornament

Since strophomenoid genera were first recognized over a hundred and fifty years ago, one of the main characters used for their separation and identification has been the shape and profile of the valves. For example, *Strophomena* itself is resupinate, and *Leptaena* and *Rafinesquina* are concavo-convex. In addition to overall valve shape, many strophomenoids have a distinctive geniculation, usually dorsally directed, in one or both valves. *Leptaena* is a classic example possessing geniculation (in this case with an interior rim often developed) in both valves. Ventrally-directed geniculation is rare, but occurs in *Altaestrophia*, *Amphistrophiella*, *Kjerulfina*, *Leptodontella*, *Luhaia*, *Odoratus*, *Strophonella*, and *Parastrophonella*. A distinctive bilobed outline is seen in various brachiopod stocks, such as the well-known dalmanelloid *Dicoelosia*, and this is known in the Strophomenoidea only in *Dicoelostrophia*. Ornamentation is very variable; most Strophomenoidea have variations of costellate ornament, but a few genera, such as *Foliomena*, *Laevicyphomena*, *Lissoleptaena*, *Lissostrophia*, and *Pholidostrophia* lack any radial ornamentation. There is some variation in this respect; for example within populations of *Mesopholidostrophia* from the Wenlock Mulde Marl of Gotland, Sweden, most individuals are apparently smooth, but in a small proportion there are faint traces of radial ornament. There are also a few genera which are generally smooth apart from a single median costa, such as *Qianomena* and *Rugoleptaena*. Running across the radial ornament and subparallel to the antero-lateral valve margins there are valve undulations termed rugae. Rugae are developed variably in many strophomenoids, and vary between very regular rugae across the whole valve disc, such as in *Leptaena*, to a minor development near the lateral margins only to be seen in gerontic members of some populations (e.g. the specimen of *Kjaerina typa* figured herein Pl. 3, fig. 2). Sometimes the rugae flow across the radial ornamentation without interruption, but in some genera stronger costellae interrupt the rugae to give a distinctive pattern such as seen in *Bellimurina* and

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ventral interarea with a covered delthyrium and irregular and finely denticulated teeth; κ, anterolateral view of the dental plates with rough and fewer crenulations not corresponding to the 'denticles' on the top of the teeth; L, *Strophomena planumbona*, based on AMNH 30248; ventroposterior view of the ventral interarea with a covered delthyrium and irregular, usually divergent 'denticles' essentially different from those in *Eostropheodonta*.
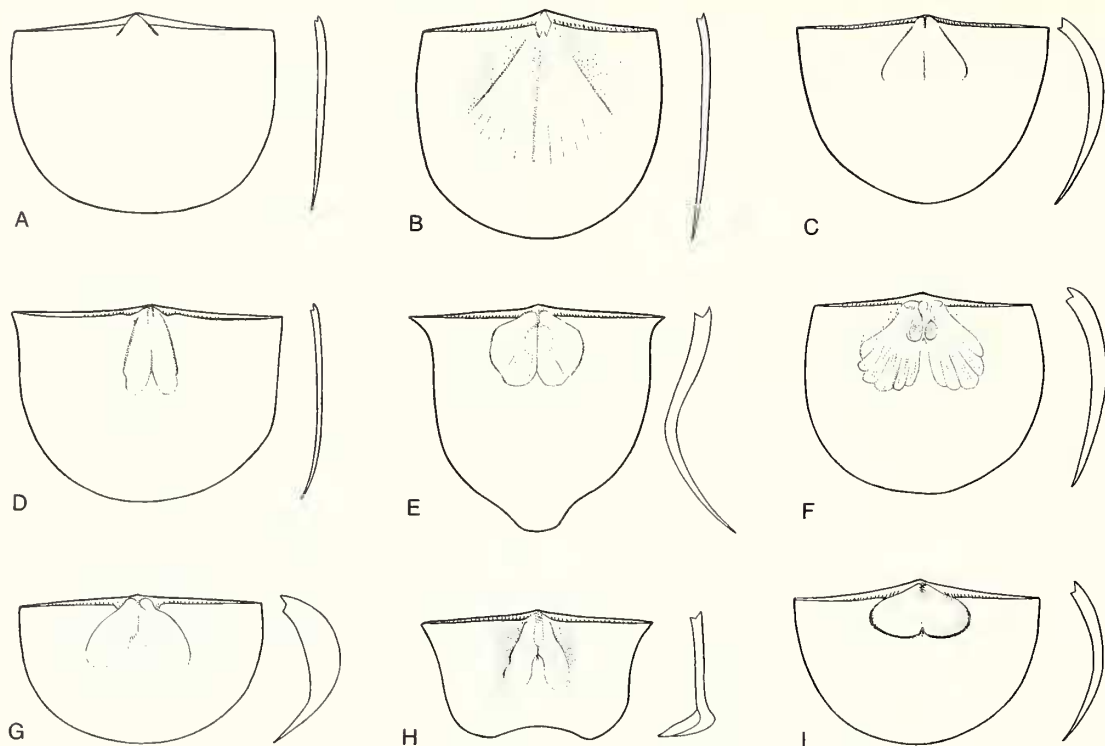
TEXT-FIG. 9. Ventral valve muscle fields, as seen in internal moulds, and characteristic lateral outlines of various denticulate strophomenoids. A, *Eostropheodonta*; B, leptostrophiid; C, mesodouvillinid; D, shaleriid; E, strophonellid; F, strophodontid; G, *Phragmostrophia*; H, *Leptodontella*; I, douvillinid.
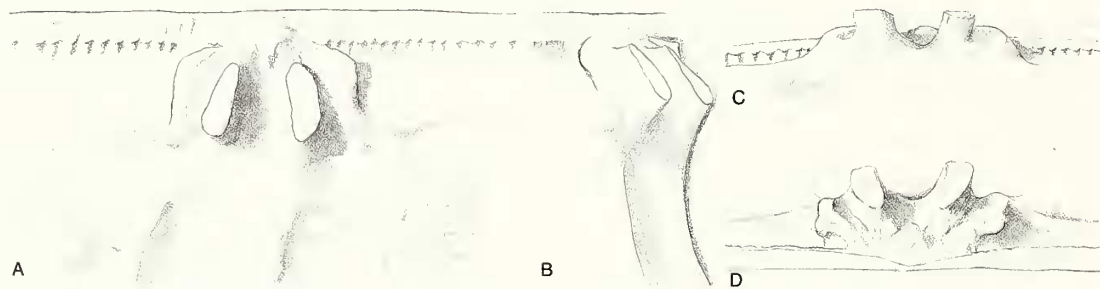
TEXT-FIG. 10. The cardinalia of *Rhytistrophia beckii*, based on AMNH 33167; ×6.

Pentlandinia. Similar patterns are also found in plectambonitoids such as *Ptychoglyptus*. Some of these interrupted rugae form interference patterns, for example the *Limbimurina* figured by Cooper (1956, p. 221, fig. 42).

CLASSIFICATION

In the past, various workers have used different criteria for allocating strophomenoids to families and subfamilies and for separating and defining genera. However, in the course of our revisions, both of the Plectambonitoidea (Cocks and Rong 1989) and of the Strophomenoidea in the present work, we have become convinced of the prime importance of the position and morphology of the

TEXT-FIG. 11. The cardinalia of *Shaleria* (*Janiomya*) *ornatella*, based on BC 13112; × 12.
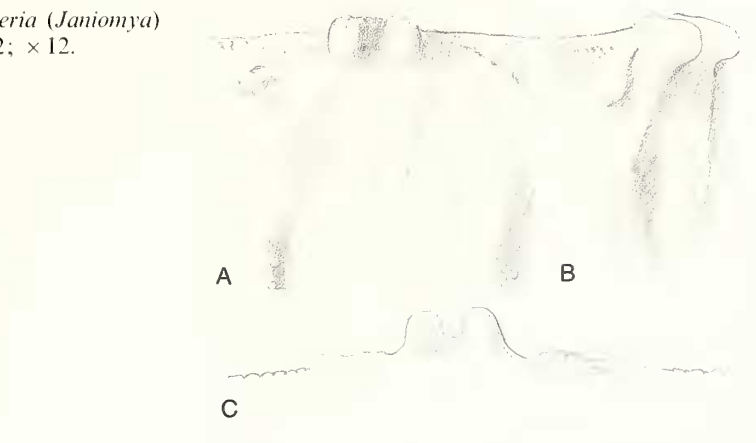
cardinalia as the most conservative and fundamental feature to be used in both the discrimination and unification of family rank groups, except within strophomenoids bearing denticulate articulation.

In most published discussions, the diagnoses of families and subfamilies have on analysis proved vague, since too many characters with too much variation have been included. In addition, many structures have neither been described precisely nor evaluated properly, and in some cases a single character has been used by an author to differentiate a new family group with no discussion or appreciation of the effects of using that character in the classification of the whole superfamilial or subordinal group. For example, we have demonstrated in the Plectambonitoidea that resupination can occur in genera related closely to others of normal convexity (Cocks and Rong 1989), but reversed convexity has been used as one of the chief methods of distinguishing two families, the Amphistrophiidae and the Strophonellidae. We try here to develop a supraspecific classification that is based firstly on the evolutionary history of the group, but which is crisply defined and possible
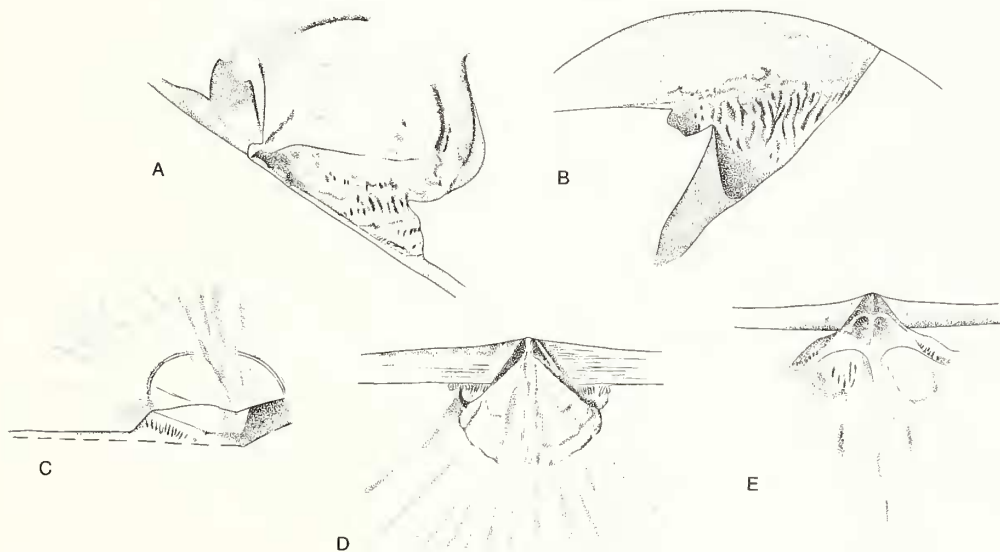
TEXT-FIG. 12. *Katastrophomena woodlandensis*. A–D, Crenulations on the teeth in the ventral valve, E, socket ridges in the dorsal valve. Note the irregular nature of the crenulations, which are homologous to true denticles. A, B, based on BB 66893; A, × 6; B, × 12; C, D, based on B 54506; × 3; E, based on BC 2184; × 3.

for other workers to use. However, we stress that there is great variability within the group, from the population level upwards.

Characters for differentiating families

We follow Cooper (1969 p. 198) in considering that 'the family characters of the genera comprising the family are based on the cardinalia of the dorsal valve and some features of the ventral valve'. Both our experience in many groups of brachiopods have convinced us that Cooper was right; the cardinalia appear to be the most conservative characters in the Orthida and Strophomenida apart from in some denticulate families. We consider that this was probably because of the vitally important function of the cardinalia and also because of the relatively small space between the two valves in the Strophomenida which hindered evolutionary development of the cardinalia which thus became a familial, rather than a generic, character in classification. This is in contrast to the Pentamerida and Rhynchonellida, where the presence of other structures and also the large space between the opposing valves gave more scope for evolutionary changes. It explains why we have been able to identify only three main types of cardinalia in the Plectambonitoidea (simple, trifid or undercut – Cocks and Rong 1989) and four types (described above as A to D) in those Strophomenoida without hinge line denticles. Types A to D form the basis of our definition of the families Christianiidae, Glyptomenidae, Rafinesquinidae and Strophomenidae. However, within those forms with denticulate hinge lines, the separate stocks modified from type B through type E to type F, and in many cases to type G. Thus we cannot separate these denticulate forms on the basis of cardinal process type. One of the bases of familial separations within those forms is the conservative character seen in the shape of the ridges bounding the ventral valve muscle fields (Text-fig. 9) taken with structures such as the median ridge and side septa which are variably developed in the dorsal valve. However, some dorsal internal structures are included in our placing of individual genera within families.

In addition, we recognize as separate families those groups of genera with denticles on the hinge line, as opposed to those which have smooth hinge lines. We do not use the term 'denticulate' for many genera (see Appendix) which have smooth hinge lines, but which have crenulations on the teeth and sockets. However, since we regard the acquisition of denticles as having occurred more than once, we do not group all the denticulate families into a single superfamily – the Stropheodontacea of many authors from Sokolskaya (1960) onwards. Denticulate hinge lines (but with denticles of varying shapes) have been recorded in many different brachiopod stocks, namely the Plectambonitoidea (e.g. *Eoplectodonta*), Chonetidina (e.g. *Eodevoniaria*), Productina (e.g. *Ctenalosia*), which are all Strophomenida, and also in Spiriferida (e.g. *Anthracospirifer increbescens*, *Spiriferinaella* and *Rastelligera*) (Cooper 1969). Only in the 'Stropheodontacea' has this character been elevated to importance in superfamilial diagnosis, which strengthens our rejection of it.

Characters for differentiating genera

Gross changes in valve morphology are recognized here at the generic level, for example resupination and clear geniculation. Occasionally we accept the presence of a substantial fold and sulcus, for example in *Esilia*; however there is much plasticity in this character in some stocks, and it is usually more applicable to differentiation at the specific rather than the generic level. In general, we do not accept variations in the ornament, for example between parvicostellate and fascicostellate, as a valid character for generic differentiation; however, the presence of radial plications and concentric rugae over the whole shell can be of generic importance and the exceptionally distinctive discontinuous costellae seen in *Nervostrophia* is also recognized. Subgeneric status is also according to the lack of finer costellae, as seen for example in *Strophonella* (*Quasistrophonella*). Within the valves the presence or absence of dental plates or socket ridges, muscle bounding ridges, ventral processes, side septa, or substantial diaphragms are used to differentiate genera. However, in the forthcoming *Treatise* volume, we intend to place many genera into synonymy, particularly in the *Leptaena* group, which have been erected on what we consider merely specific or even subspecific criteria.

Characters for differentiating species

These vary between genera, but a useful initial concept is that there are seldom more than one species of the same genus in the same bedding plane. Populations of strophomenoids are very often extremely variable, and it is our experience that the greater the number of specimens collected from a single horizon then the less clearcut the differentiation of the species becomes. Thus no further new species should be erected without firstly, a clear knowledge of the internal structures of both valves, and secondly, an appreciation of the

TEXT-FIG. 13. *Biparetis paucirugosus*. A, based on OGS 6716; posterior view of cardinalia showing crenulations on the posterior facets of the socket ridges. B–C, based on OGS 6703; oblique view of ventral valve; B, showing fine 'denticles' on the dorsal facet of the teeth; C, showing crenulations on the posterior part of the antero-median facets of the teeth. All × 6.

variation present at the type locality. For example, *Eostropheodonta hirnantensis* has both fascicostellate and parvicostellate ribbing in different individuals at the type locality (Temple 1965, p. 411, pl. 17, fig. 6; pl. 18, fig. 7), yet this character has been cited as of familial importance by some authors (e.g. Harper and Boucot 1978, p. 101). The detailed characters for the discrimination of species include details of ornament, relative dimensions of shell shape, and relative proportions of internal structures. However, relative convexity should be used with care; in some populations there is little variability, but in others it is very substantial (e.g. in *Brachiprion arenacea* measured by Cocks 1967, p. 259).
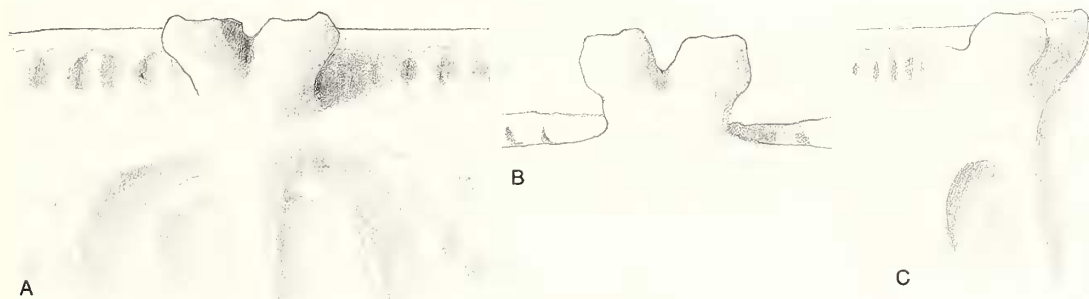
TEXT-FIG. 14. The cardinalia of *Pholidostrophia nacrea*, based on AMNH 37211; × 12.

Origin of the strophomenoids

The origin of the strophomenoids is obscure in detail. They are known from several localities in rocks of Llanvirn age: for example, *Trotlandella loki* Neuman *in* Neuman and Bruton (1974, p. 95) from a Whiterock facies block, Holanda, Norway; *Murinella* sp., '*Macrocoelia*' *llandeiloensis elongata* and *Christiania elusa* from the Llanvirn of central Wales (Lockley and Williams 1981); and possibly *Kirkina millardensis* Salmon (1942, p. 599) from the Pogonip Limestone of Utah, USA. There are hitherto no documented strophomenoids from Arenig strata. However, in redescribing the plectambonitoid *Toquimia kirki* from the Antelope Valley Limestone of Llanvirn age from Utah, Ross (1970, p. 64, pl. 8, fig. 17) described a sectioned specimen in which the cardinal process appeared bilobed. This was confirmed by G. A. Cooper (pers. comm.). Bearing in mind that *Toquimia* was assigned to the Leptellinidae because it, like the rest of the family, had a cardinal process that was not undercut, and had no bema or side septa (Cocks and Rong 1989, p. 102), and that those family characteristics are also seen in the earlier strophomenoids, it seems reasonable to postulate that the strophomenoids probably had their ancestors within the Leptellinidae. However, in the Sandaokan Formation of the Ordos Platform, northern part of Shaanxi Province and extending into the southern part of Inner Mongolia, part of the north China plate, an undescribed strophomenoid has been found in Liu Di-yong and Fu Li-pu which is of undoubted Arenig age, since late Arenig conodonts succeeded by early Llanvirn graptolites overly the formation in a structurally uncomplicated section. The specimens are preserved in limestone and the pseudopunctae are clearly visible. The bilobed cardinal process is small and of Type A, the socket ridges are curved posterolaterally and there are weak side septa in the larger specimens, thus this undescribed species is referrable to the Strophomenidae.

THE FAMILIES AND SUBFAMILIES

The Superfamily Strophomenoidea differs from other pseudopunctate brachiopods in its bifid cardinal process (which differentiates it from the Plectambonitoidea) and its lack of spines (which differentiates it from the productoids and chonetoids). Early orthotetoids are impunctate. We include both denticulate and non-denticulate forms within the superfamily. Its included families are as follows.

Family **Strophomenidae** King, 1846. Hinge line non-denticulate. Cardinal process lobes robust, often subcircular (Type A), situated on the posterior part of a well-developed notothyrial platform. Discrete, strong socket ridges often curved round laterally at their ends. The subfamily Strophomeninae King, 1846, has absent or very weak side septa in contrast to the subfamily Furcitellinae Williams, 1965, in which dorsal muscle field bounding ridges and side septa are well developed (Text-fig. 15). Typical strophomenine genera are *Actinomena, Dactylogonia, Holtedahlina, Longvillia,* and *Strophomena*; typical furcitellines are *Biparetis, Costistrophomena, Cyphomena, Furcitella, Katastrophomena,* and *Pentlandina*.
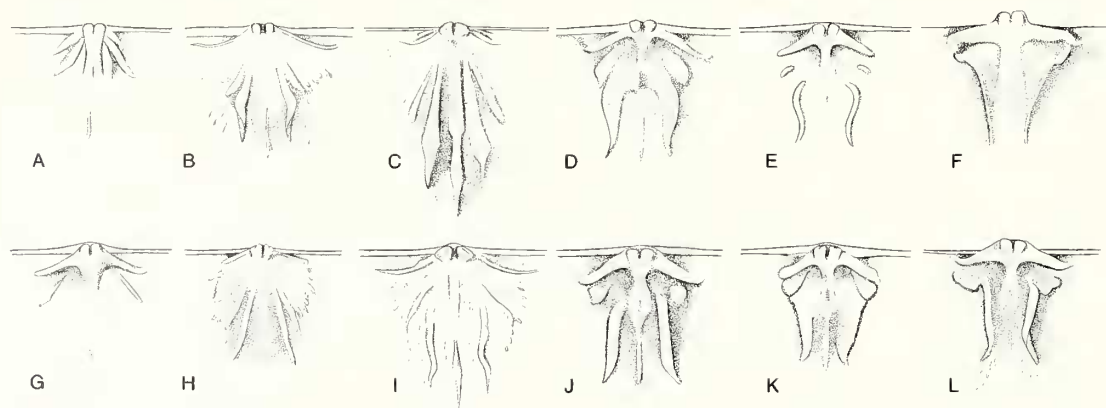
TEXT-FIG. 15. Dorsal interiors showing the variation in genera of the Furcitellinae. A, G, *Furcitella*; B, H, *Dactylogonia*; C, I, *Oepikina*; D, J, *Pentlandina*; E, K, *Katastrophomena*; F, *Biparetis*; L, *Quondongia*.

Family **Rafinesquinidae** Schuchert, 1893. Hinge line non-denticulate. Cardinal process lobes usually elongate or plate-like and they remain entirely discrete throughout ontogeny (Type B). Notothyrial platform variably developed. Socket ridges straight, often thinner and smaller than the Strophomenidae. The subfamily Rafinesquininae Schuchert, 1893, lacks geniculations and rugae (except posterolaterally) whilst the subfamily Leptaeninae Hall and Clarke, 1894, is geniculate and usually rugate over most of the shell. Typical rafinesquinine genera are *Hedstroemina, Kjaerina, Rafinesquina,* and *Rhipidomena*; typical leptaenines are *Hingganoleptaena, Kjerulfina, Leptaena, Lissoleptaena,* and *Rugoleptaena*.

Family **Glyptomenidae** Williams, 1965. Hinge line non-denticulate. Small cardinal process lobes at or largely posterior to the hinge line (Type C). Socket ridges fused directly to the lateral bases of the cardinal process lobes. Notothyrial platform usually absent, and there is often a concave area immediately anterior to the cardinal process lobes. The subfamily Glyptomeninae Williams, 1965, lacks side septa in the dorsal valve and the subfamily Teratelsaminae Pope, 1976, possesses them and a high median dorsal septum. Typical glyptomeninine genera are *Bystromena, Glyptomena, Paromalomena, Platymena,* and *Rhactomena*. The Teratelasminae is monogeneric.

Family **Foliomenidae** Williams, 1965. Hinge line non-denticulate. Cardinal process like the Glyptomenidae (Type C), but family without radial ornament, lacking dental plates, ventral muscle field small and bilobed, and with a pair of close and narrowly divergent side septa. The only firm attributed genus is *Foliomena* (= *Jielingia*).

Family **Christianiidae** Williams, 1953. Hinge line non-denticulate. Low cardinal process with lobes very close together and fused at their bases (Type D). Socket plates often elevated anteriorly from the valve floor. Two pairs of distinctive large septa present in the dorsal valve. Ventral valve muscle field small and bilobed. *Christiania* (= *Christianella*) is the only genus.

Family **Leptaenoideidae** Williams, 1953. Hinge line non-denticulate. Bizarre forms with ventral valve attached to the substrate by cementation. Dorsal interior only known in *Leptaenisca*, which has strong, ventrally-directed cardinal process lobes. Thin low short socket ridges close to the cardinal process. The genera attributed are *Leptaenisca*, *Leptaenoidea*, *Leptaenomendax*, and *Liljevallia*.

Family **Amphistrophiidae** Harper, 1973. Hinge line denticulate. Cardinal process variable. Lacks dental plates. Ventral muscle field semi-elliptical in outline, bounded laterally by curved bounding ridges (except *Eoamphistrophia*). Dorsal muscle field bounded posterolaterally by low ridges extending anteriorly from the socket ridges. No side septa. The subfamily Amphistrophiinae is resupinate and the Mesodouvillininae Harper and Boucot, 1978, is concavo-convex. Typical amphistrophiine genera are *Amphistrophia*, *Devonamphistrophia*, and *Eoamphistrophia*; typical mesodouvillinines are *Maoristrophia*, *Mclearnites*, *Mesodouvillina*, and *Sinostrophia*.
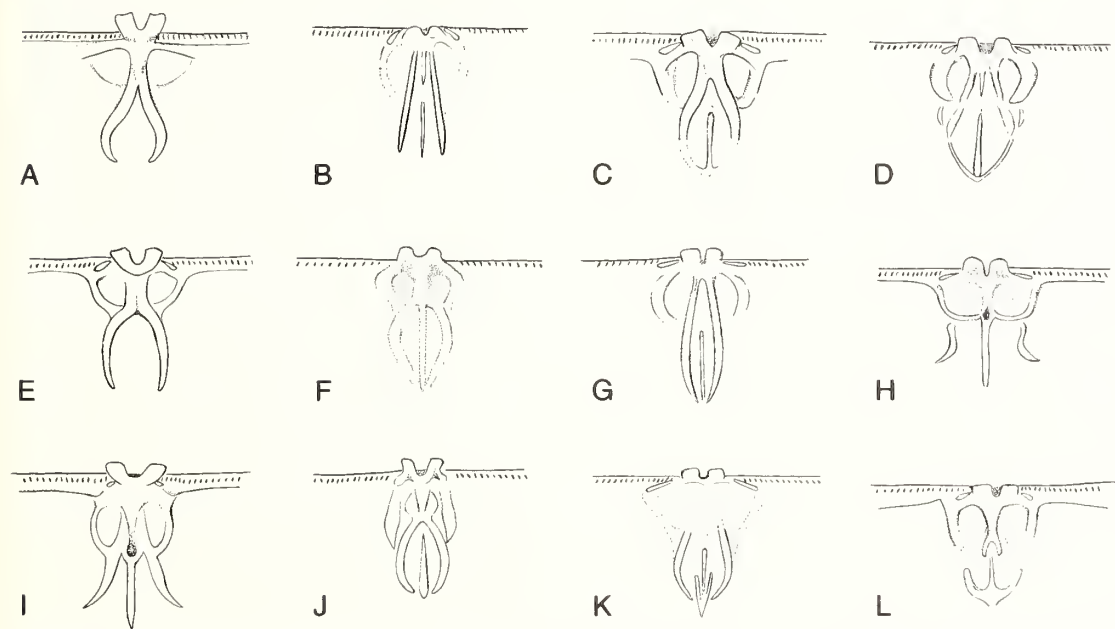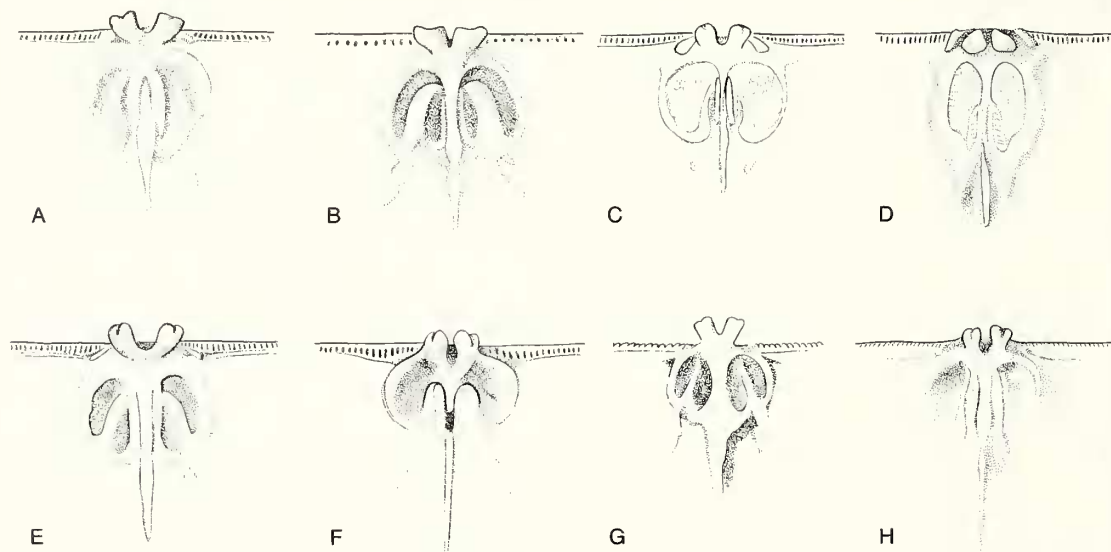

TEXT-FIG. 16. Dorsal interiors of genera of the Protodouvillininae. A, *Protodouvillina*; B, *Douvillinella*; C, *Malurostrophia*; D, *Nadiastrophia*; E, *Douvillina*; F, *Cymostrophia*; G, *Planodouvillina*; H, *Phragmostrophia*; I, *Radiomena*; J, *Telaeoshaleria*; K, *Crinistrophia*; L, *Taemostrophia*.

Family **Douvillinidae** Caster, 1939. Hinge line denticulate. Lacks dental plates (except *Crinistrophia*). Ventral muscle field bilobed and well impressed, usually with bounding ridges laterally and anteriorly. Side septa present. Cardinal process lobes directed ventro-posteriorly and posteriorly. Small socket ridges. The subfamily Douvillininae has an elevated ventral muscle field with overhanging bounding ridges meeting anteriorly; the subfamily Protodouvillininae Harper and Boucot, 1978 (= Douvinellinellinae and Teichostrophiinae, both Harper and Boucot 1978) is like the Douvillininae but without an elevated muscle field; the subfamily Leptodontellinae Williams, 1965, has an elongated muscle field and the widest part of the dorsal valve muscle field occurs anteriorly rather than posteriorly and side septa are poorly developed; and the monogeneric subfamily Dicoelostrophiinae Wang and Rong, 1986, has a sharply indicated, bilobed anterior commissure and two pairs of high septa in the dorsal valve. Typical douvillinines are *Douvillina*, *Douvillinaria*, and

Douvillinoides; typical protodouvillinines are *Cymostrophia*, *Douvillinella*, *Malurostrophia*, *Protodouvillina*, and *Telaeoshaleria*; and typical leptodontellines are *Leptodontella*, *Parastrophonella*, *Sulcatostrophia*, and *Zophostrophia*.

Family **Leptostrophiidae** Caster, 1939. Hinge line denticulate (except *Eostropheodonta*, see above; Text.-fig. 8). Lateral profile biplanate or gently concavo-convex. Triangular ventral muscle field, open anteriorly. Cardinal process lobes usually ventrally directed, but rarely posteriorly. Side septa generally absent. Typical leptostrophiids include *Brachyprion*, *Gibberostrophia*, *Leptostrophia*, *Mesoleptostrophia*, and *Protoleptostrophia*.

Family **Strophodontidae** Caster, 1939. Hinge line denticulate. Subcircular to suboval ventral muscle field strongly impressed, but without bounding ridges anteriorly and often laterally. Dorsal muscle field usually elevated on a platform with bounding ridges. Dorsal median septum and side septa usually, but not always, present. Typical strophodontids include *Galateastrophia*, *Lissostrophia*, *Pholidostrophia*, *Strophodonta*, and *Strophonelloides*.

TEXT-FIG. 17. Dorsal interiors of genera of A–G, the Strophodontinae, and H, Mesodouvillinae showing the origin of the Strophodontinae. A, *Cymbistropheodonta*; B, *Pholidostrophia*; C, *Asturistrophia*; D, *Boucotstrophia*; E, *Strophodonta*; F, *Parapholidostrophia*; G, *Galateastrophia*; H, *Mesodouvillina*.

Family **Eopholidostrophiidae** fam. nov. See below.

Family **Shaleriidae** Williams, 1965. Hinge line denticulate. Parallel-sided and elongate ventral muscle scars with lateral bounding ridges. Dorsal median ridge present which commonly bifurcates anteriorly. Typical shaleriids include *Shaleria* and *Shaleriella*.

Family **Strophonellidae** Caster, 1939. Hinge line denticulate. Ventral muscle field subquadrate and often flabellate, with well developed bounding ridges (except in *Eostrophonella*). Resupinate. Typical strophonellids include *Eostrophonella* and *Strophonella*.

EVOLUTIONARY TRENDS

Like other groups of brachiopod, within most of the Strophomenoidea there are detailed evolutionary trends; however, most described trends have been concerned with denticulate families and genera. Williams (1953a) suggested the following 'strophodontoid' trends: (1) the dental plates

fusing with the denticular plates and the denticles spreading by increment along the hinge line; (2) the ventral process becoming larger with a corresponding closing of the delthyrium; (3) the socket plates becoming abbreviated; (4) the cardinal process becoming more massive and growing in a posterior direction above the chilidium which became progressively degenerate; and (5) the muscle scars becoming better defined. For the latter, Cocks (1967) described the gradual relative widening of the ventral muscle field in *Brachyprion compressa* from the early Aeronian to the late Telychian. Harper and Boucot (1978) reviewed these trends in detail and also noted an increase in shell size up to the Devonian. These general trends can be recognized as occurring at different rates and in different times within several different and sometimes unrelated stocks. From the taxonomic point of view the two most important trends appear to be the acquisition of denticles, firstly in the cardinal area and subsequently along the entire hinge line, and the change of cardinalia. In this section we also deal with variation in and modifications to the dental plates, pseudodeltidia and the muscle fields of various families within the Strophomenoidea.

Evolutionary trends in the strophomenoids have not been well understood, since there is much variation of many features in some groups and a considerable number of the genera known have not been correctly synonymized. Even though the evolutionary history of the 'strophodontoids' has been far better known than in strophomenoids (Williams 1953*a*; Harper and Boucot 1978) the transformation stages to 'strophodontoids' are still not so clear that it is known whether the 'strophodontoids' are monophyletic or polyphyletic. The original strophomenoid diversification occurred within a short time, with the earliest known representatives of christianiids, glyptomenids, leptaenids, rafinesquinids and strophomenids appearing between the late Arenig and late Llanvirn; in fact the only non-denticulate groups to appear later were the foliomenids and the leptaenoideids. Thus there was an early and rapid differentiation of the critical taxonomic character, the cardinalia, and a great generic diversification during Llandeilo and Caradoc times.

Denticulation

After the differentiation of the cardinalia, some of the Strophomenidae underwent early experimentation in the development of denticulation (Text-fig. 8). There are many Caradoc–Ashgill taxa which bear crenulations and even denticles (see Appendix), and they have the following features: (1) the denticles may be present but are always weak; they may be regular (such as the few denticles in *Dunnmuckina donax*) or irregular (such as in *Strophomena planumbona*; Text-fig. 3) and can sometimes be very fine (e.g. about fourteen to sixteen microdenticles in *Biparetis paucirugosus*; Text-figs 8, 13); (2) the crenulations are present on the posterior faces of the socket ridges rather than on the posterior margins of the sockets, and are also present on the median-anterior faces of the teeth, usually between two to six in number; (3) the numbers of denticules and crenulations in the ventral valve are often strongly inconsistent; (4) development of the crenulations and denticles is variable, and can be sporadic in the same population; sometimes they are only seen in either the ventral valve or the dorsal valve. Occasionally, a few denticles can be seen in the posterior margin of the sockets (as in *Strophomena filitexta*) and accessory socket ridges with crenulations occur (as in *Oepikina septata*; Pl. 2, fig. 8). During Silurian time, strophomenids declined in both number and diversity. The denticulation in a few strophomenids, such as *Katastrophomena woodlandensis* (Text-fig. 12), still showed the characters of their ancestors. Weakness, irregularity and instability of development of the denticles and crenulations in the Strophomenidae indicate that their adaptive experimentation in this feature was unsuccessful and it can be concluded that no taxon of the family Strophomenidae gave rise to any 'strophodontoids'.

The Leptaeninae is the longest-lived subfamily of the strophomenoids, since it ranged from the Llanvirn to the Carboniferous (Namurian). Many taxa of this subgroup, especially *Leptaena* itself in the Ordovician and Silurian, and even some species of *Leptagonia* in the Carboniferous, also underwent an adaptive experiment in the development of the crenulations and denticles (see Appendix). The crenulations have usually been observed in the dorsal valve where they are located on the posterior facets of the socket ridges, and no crenulations have been found in the posterior margins of the sockets. For instance, in *Mackerrovia lobatus*, from the Telychian of Shropshire, UK, there are about twelve to sixteen irregular and undulate crenulations on the posterior faces of the socket ridges, for example in BC50573. This number of crenulations is more than its Ordovician ancestors, which usually bear two to five crenulations on the posterior faces of the socket ridges. Again, the crenulations can be developed sporadically in the same population. Sometimes the crenulations are quite strong (e.g. Havlíček 1967, pl. 15, fig. 16 for *Leptaena depressa*), but usually they are weak. Thus in the

development of true denticulation the *Leptaena* subgroup, like the Strophomenidae, was also unsuccessful and no 'strophodontoids' were derived from the Leptaeninae.

The Glyptomenidae includes only a few taxa with crenulations, perhaps because most of the later representatives of the group (such as *Bystromena* and *Paromalomena*) are small and did not develop crenulations to strengthen their articulation; however, a few earlier and larger taxa, such as *Mjoesina moorei* Mitchell, 1977, do bear crenulations. This group declined in the Silurian, consisting only of *Linostrophomena* and *Qianomena* in South China in the early Aeronian and Telychian (Rong and Yang 1981), which possess no crenulations. Like the Leptaeninae and Strophomenidae, the Glyptomenidae do not seem probable ancestors of the 'strophodontoids'.

The earliest known strophomenoids with crenulations (mainly pits) on the antero-median faces of the teeth and on the posterior faces of the socket ridges are known in rocks of Llanvirn age, for example '*Macrocoelia*' *llandeiloensis elongata*, which is a rafinesquinid. Thus the rafinesquinids were possibly the first family to experiment in the development of denticulation, and this occurred in a very early stage of their evolutionary history. During the first stage of denticular development (mainly from the Llanvirn to the Caradoc) rafinesquinids followed the same pattern as the Strophomenidae, in which denticles are present only in the ventral valve and are usually regular but weak, and are located in the same position as those of the Strophomenidae. There are many taxa with such immature denticulation (Appendix). During this stage, in rafinesquinids and also in strophomenids and glyptomenids, the delthyrium is covered in one of three ways: (1) completely, by a well-developed pseudodeltidium (such as in *Maakina kulinnensis, Oepikina? walliensis; Strophomena planumbona* (Pl. 1, figs 5–6), and *Trigrammaria virve*); (2) partly, by a pseudodeltidium (such as in *Biparetis pancirugosus, Furcitella plicata, ' Macrocoelia' stenomuscula* and *Ranfinesquina alternata* (Pl. 2, fig. 7); (3) apically, by a small pseudodeltidium (such as in *Actinomena orta, Bellimurina tenuicorrugata, Longvillia grandis* and *Mjoesina moorei*). The earliest denticulate forms have an open delthyrium, which may have an apical pseudodeltidium. Therefore, the partial or complete absence of a pseudodeltidium appears to have favoured the acquisition of denticulation.

In the second stage, during late Caradoc and Ashgill times, there occurred some taxa in which the delthyrium was open, with the pseudodeltidium either very small or absent, apart from some forms such as *Eostropheodonta* spp. (= *Aphanomena, Eoleptostrophia* and possibly *Hibernodonta*) and *Origostrophia fragilis* (Mitchell, 1977) with a very small apical cover which may have been supported by a faint ventral process. This stage is characterized by a stable development of both crenulations and denticules in the ventral valve, which Williams (1951) called the denticular plates, emerging from beneath the lamellar layer on either side of the delthyrium. Both denticles and crenulations are seen in the ventral valves on the denticular plates and the median anterior part of the teeth. These should have counterparts in the dorsal valve. However, although there are counterpart crenulations on the posterior face of the socket ridge in the dorsal valve, there are no counterpart denticles to those on the ventral valve denticular plate. Moreover, the denticles in the ventral valve denticular plate are regular and relatively strong, although the numbers of the denticles and crenulations on the different faces of the teeth are usually different. More importantly, both denticles and crenulations in the ventral valve are usually stable in the same population. This applies to many species, for example, *Eostropheodonta parvicostellata* from the Hirnantian beds in South China (Rong 1984). From the point of view of speciation, the establishment of denticulation in the whole population is critical in the transformation of the strophomenoids to 'strophodontoids'. *Eostropheodonta* had wide distribution and a variety of other

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Figs 1–7, 9–11. *Strophomena planumbona* (Hall); Hudson River Group (late Caradoc); Cincinnati, Ohio, USA. 1–3, 5, AMNH 30247, lectotype; dorsal, ventral, lateral and posterior views of conjoined valves; × 1·5 (except 5, × 2). 4, 6, 10, AMNH 30248; ventral, postero-ventral and enlarged views of ventral interior; 4, × 1·5, 6, × 2, 10, showing crenulations on the teeth; × 6. 7, AMNH 918/5a; dorsal valve interior; × 1·5. 9, AMNH 918/5b; dorsal valve interior; × 1·5. 11, BB 6428; oblique view showing crenulations on the inside of the teeth in the ventral interior; × 8.

Fig. 8. *Strophomena vetusta* James; same locality as above; AMNH 918/5c; enlarged view of cardinal process; × 6.

Fig. 12. *Katastrophomena woodlandensis* (Reed); Woodland Formation (lower Llandovery; Rhuddanian), Woodland Point, south of Girvan, Strathclyde, Scotland; BC 2170; enlargement of natural internal mould of ventral valve to show impression of crenulations on the antero-median face of the teeth; × 10.
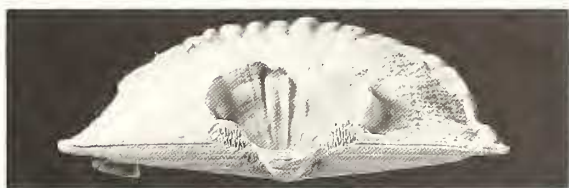
PLATE 1

RONG and COCKS, *Strophomena, Katastrophomena*

denticulate genera were undoubtedly derived from it by modification of both cardinalia and denticulation, together with other characters. In general, these were relatively flat genera of moderate overall size, a relatively open delthyrium, dental plates and occasionally a weak ventral process. The muscle scars were usually faint. At the beginning of the Llandovery, *Palaeoleptostrophia jamesoni* may have been derived from *Eostropheodonta* by the loss of dental plates, and this became a main stock which later gave rise to many other genera including *Mesoleptostrophia*.

Williams (1953*a*, p. 8) suggested that the earliest known 'strophodontoids' occurred in the Ashgill and Lower Llandovery of Britain. In these forms, there are denticular plates which are fused along their dorsal edges to a pair of short dental plates. We confirm that premature denticular plates (although not true hinge line denticles) occur in many taxa of most groups in strophomenoids in the later Ordovician (see Appendix). The most important development in the origin of the denticulate forms is the development of denticles on the top of the teeth; but to be accepted as such the denticles must be as strong and regular as those in the later stocks, and this is often associated with the loss of dental plates. Before Hirnantian times, there had occurred several taxa of 'strophodontoids' with no dental plates. They are (1) *Origostrophia fragilis* (Mitchell 1977, p. 116, pl. 25, figs 1–13) which possesses thin but very wide denticular plates bearing five to sixteen denticles extending along the hinge line for up to one-half of its width, and possesses a relatively strong ventral process; (2) *Eopholidostrophia portlocki* (Reed) (Mitchell, 1977, p. 114, pl. 26, figs 1–13); and (3) Stropheodontinae gen. et sp. indet. of Mitchell (1977, pl. 25, figs 14–20) which also bear denticles on their teeth. They are all from the lower to middle Ashgill Killey Bridge Formation, Pomeroy, Ireland. In addition, *Eopholidostrophia matutinum* (Lamont) from the Lower Drummuck Group of Girvan, Scotland, also has denticles on the teeth (Harper *et al.* 1967) although Hurst (1974, p. 301) observed that there are no denticles in *E. matutinum* but occasionally the teeth bear extremely fine elongate striations. We have examined the type specimens of *E. matutinum* and confirmed the conclusion made by Harper *et al.* (1967). We consider that the latter situation indicates an initial stage of one 'strophodontoid' stock, i.e. the eopholidostrophiid, a similar developmental trend to that seen in *Eostropheodonta*. But the origin of this stock is still unknown. It is important to note that all the taxa mentioned above with denticles or crenulations in their ventral valves, and with no dental plates, bear no denticles on the hinge line in the dorsal valve (that is, on the posterior margins of the sockets), although the socket plates are crenulated. Thus this is a distinctive feature of the initial stage in the evolution of denticulate Strophomenoidea.

The third stage in the evolution of denticulation was mainly in early and middle Llandovery times, when many taxa evolved which bear denticles in both valves for the first time, although others bear denticles only in the ventral valve and they are absent in the dorsal valve apart from crenulated socket ridges. There are three stocks in which denticles occur in both valves; *Eopholidostrophia sefinensis ellisae*, for example in BB95790, *Eostrophonella eothen* (Text-fig. 5) and *Palaeoleptostrophia jamesoni*, for example in BC2454 (Pl. 6, figs 3–5), all from the Rhuddanian of Britain. However, development of denticles on the posterior margin of the sockets can be present or absent in the same population, indicating an immature developmental stage. The number of denticles and crenulations on the opposite faces of the teeth are nearly the same by this stage in any one individual, and in successive stocks they became identical in number and continuous with each other round the corners of the teeth. In *Eostropheodonta*, the denticles in the dorsal valve are not developed in many species, such as in *E. beechhillensis* (Harper 1973, p. 35), *E. mullochensis* (for example in B73006) and *E. multiradiata* (Temple 1987, p. 81), all Rhuddanian in age, and *E. densa* (Rong and Yang 1981, p. 175) and *E. voraginis* (Cocks 1967, p. 253) from the Aeronian. *Palaeoleptostrophia?* sp. (*Aphanomena* sp. of Harper and Boucot 1978, pl. 1, fig. 2*a–c* from the upper Aeronian of Quebec) has about eight or nine denticles on the posterior margin of the socket; however, no ventral valves are illustrated by Harper and Boucot, and thus the presence or absence of dental plates and the generic attribution is uncertain. Thus the third stage was an intermediate

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EXPLANATION OF PLATE 2

Figs 1–7. *Rafinesquina alternata* (Hall); Cincinnati Group (upper Caradoc), Cincinnati, Ohio, USA. 1–3, 5–7, B 39912; dorsal interior. 1, dorxal view; × 1. 2, latex cast of dorsal interior, viewed obliquely showing crenulations on the posterolateral facet of the socket plate; × 5. 3, latex cast of dorsal interior, for comparison with material preserved as only internal moulds; × 2. 5–7, anterior, lateral and postero-dorsal views of the cardinalia; × 5. 4, BB 13088; lateral view of the cardinalia of another specimen; × 5.

Fig. 8. *Oepikina septata* Salmon; Lebanon Formation (Caradoc), roadcut on US Highway 41, 14·5 km SE of Murfreesboro, Tennessee, USA; USNM 117829c, holotype; posterior view of dorsal valve; × 8.

PLATE 2

RONG and COCKS, *Rafinesquina, Oepikina*
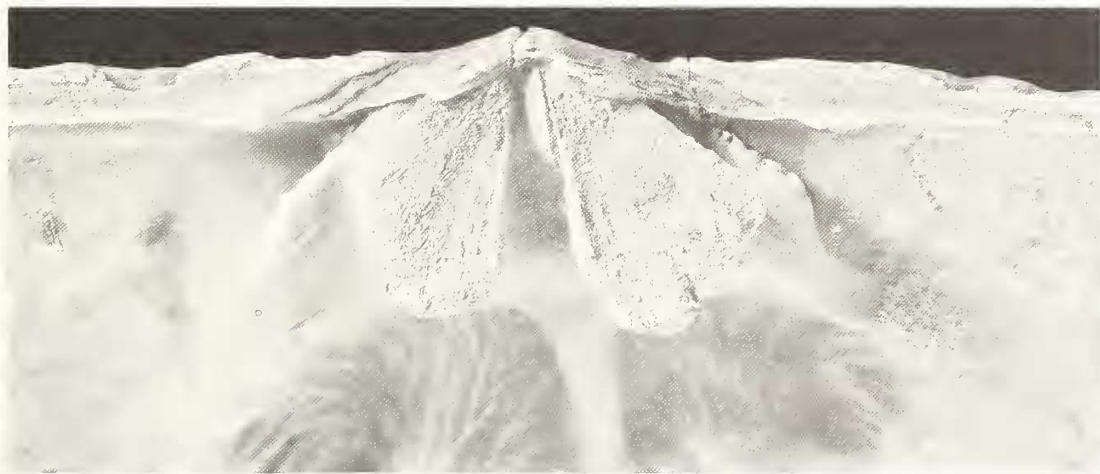
but distinctive stage in which the establishment of denticulation was earlier in *Eopholidostrophia*, *Eostrophonella* and *Palaeoleptostrophia* than in *Eostropheodonta*. Establishment of denticulation is usually associated with the open delthyrium noted above, loss of dental plates (in most genera), a faintly impressed muscle field with no bounding ridges in the ventral valve, and a weakly impressed muscle field lacking any traces of trans-muscle septa in the dorsal valve.

In the fourth stage (mainly in late Aeronian and later time), the establishment of denticulation was completed in which almost all taxa of the denticulate families bear denticles in both ventral and dorsal valves. As time went by, denticular plates became larger in general, with more denticles on them, and the denticles started to spread gradually and progressively along the hinge line. The general trend in evolution of denticulation in the Silurian was that the more denticles present, the younger the age of the taxon in the same stock, assuming that the absolute size was comparable. We do not put any great systematic value on the absolute number of the denticles or on the proportion of the hinge line occupied by them at any time in the history of the stock, since, as suggested by Williams (1953*a*), the increasing denticulation of the hinge line was progressive ontogenetically as well as phylogenetically. In a very small specimen of the Devonian *Strophodonta* sp. which Williams (1953*a*, pl 2, fig. 9) sectioned, only three denticles were present on either side of the delthyrium, leaving an appreciable length of the hinge line free of them; although the hinge line of the adult forms are nearly completely denticulate. However, it is a general evolutionary trend that early forms have fewer denticles in adult stages and later forms numerous denticles. Crenulations on the posterior faces of the socket ridges, when the ridges are present, are conservative structures, which occurred as early as the Llanvirn in strophomenoids and are also present on Silurian forms – for example in *Amphistrophia* (BC4363), *Palaeoleptostrophia* (BC2471) and *Protoshaleria* (BC13112), and in later Devonian forms such as *Megastrophia* (BB16709 Pl. 7, figs 1–2), *Protodouvillina* (AMNH 37217), *Strophodonta* (BB16568), and *Strophonelloides* (B41635; Pl. 6, fig. 9). This may indicate the importance of crenulations in strengthening articulation. In most stocks, the boundary between the third and fourth stages occurred at some time in the Aeronian. Specimens from upper Aeronian rocks (*sedgwickii* Zone) mostly bear well established denticulation although the number of denticles in the dorsal valve may be small. All the 'strophodontoid' species we have observed from Telychian rocks possess denticles in the dorsal valve.

The suborder Strophomenidina (including plectambonitoids and strophomenoids) possess deltidiodont rather then the cyrtomatodont hinge teeth which are more efficient in articulation than deltidiodont teeth (Jaanusson 1971). To have the function of keeping the position of the axis of rotation fixed along a long hinge line in strophomenoid evolutionary history, it was necessary to form accessory structures, such as crenulations and denticles, which were developed to fulfil the same function when the teeth became reduced. Thus the denticles functioned as interlocking devices to prevent the valves skewing sideways. Almost no group with cyrtomatodont teeth possesses denticles along the hinge line. The first accessory structures were the crenulations in both the posterior faces of the sockets and the median-anterior part of the teeth in many taxa of strophomenoids (see Appendix). However, all of these stocks were unsuccessful in evolving denticulate hinge lines with the exception of the Rafinesquininae. Stability of the development of denticulation in a population appears to have been the critical factor for the transformation. Denticles first appear on the denticular plates in the ventral valve and subsequently spread laterally along the hinge line. The dorsal valve always acquired denticles later in the history of each stock (Text-fig. 18). This was to achieve a tight interlocking arrangement to maintain the axis of rotation just along the hinge line at all positions of opening or closing the shell, and to avoid transverse and longitudinal movements of the valves relative to each other. The establishment of denticulation, which seems to have been a new advantageous construction, led to a radiation in the Silurian and Devonian. However, although the denticulate families survived the latest Ordovician ice age, they did not escape the Frasnian–Fammenian mass extinction. This was perhaps because either (1) in the early stage of their

EXPLANATION OF PLATE 3

Figs 1–2. *Kjaerina typa* Bancroft; Cheney Longville Flags (Caradoc: Longvillian), 110 m east of Woolston Quarry, Shropshire, England; BC 13405; natural internal mould and latex cast of dorsal interior; × 8.

Figs 3–5. *Kjaerina bipartita* (Salter); Chatwall Sandstone (Caradoc), Harnage Grange, near Cressage, Shropshire, England; BC 10874; natural internal mould and latex cast of dorsal interior; × 6.

Figs 6–7. *Oepikina septata* Salmon; Lebanon Formation (Caradoc), roadcut on US Highway 41, 14·5 km SE of Murfreesboro, Tennessee, USA; USNM 117829c, holotype; dorsal and anterior views of dorsal interior; × 8.

PLATE 3

RONG and COCKS, *Kjaerina, Oepikina*

evolutionary history they had great vitality and their novelities, especially the establishment of denticulation, were very favourable to their life habits; or (2) in the later stages of their history they did not adjust to the changing environments and, although they developed existing structures, such as strong forked, posteriorly directed cardinal process lobes there was not enough space for a more developed cardinal process. Thus the 'strophodontoids', like atrypoids and pentameroids, became extinct in the early Fammenian when the ecosystems became impoverished in ecological diversity and in overall species abundance, and it was only their more generalized strophomenoid relatives within the leptaenines which survived into the Carboniferous.

The loss of dental plates in different denticulate stocks also occurred at different times, but occurred mostly before the Wenlock. The earliest known taxa lacking dental plates are *Origostrophia fragilis* and three other species in the lower Ashgill (Mitchell 1977). No taxa lacking dental plates have been recorded from the upper Ashgill and the widespread *Eostropheodonta* bears a pair of dental plates, although these are occasionally vestigial (Rong 1984). At the beginning of the Llandovery, a distinctive genus, *Palaeoleptostrophia* gen. nov. (Pl. 4, fig. 9; Pl. 6, figs 1–5) which was probably derived from *Eostropheodonta*, bears no dental plates and represents a new stock which in turn later gave rise to *Brachyprion* (Pl. 5, fig. 5), *Mesoleptostrophia* (Text-fig. 18) and other genera. Another stock is represented by *Eopholidostrophia* and its close relative *Origostrophia*, which lack dental plates and are known from the Ashgill (*E. portlocki*, *E. matutinum* and *O. fragilis*). *Eomegastrophia* has dental plates but is known from the upper Aeronian (Cocks 1967) and we have found that individuals both with and without dental plates can be seen in the topotype population of *E. ethica* from Shropshire. The earliest *Protomegastrophia*, which lack dental plates, are known from the Telychian, for example *P. prima* and *P. profunda* (Harper and Boucot 1978). The ancestor of *Amphistrophia*, *Eoamphistrophia whittardi*, also lacks dental plates and occurs in the Telychian. All the other denticulate genera in the upper Silurian and Devonian lack dental plates apart from: (1) *Eostropheodonta* sp. which has a pair of very thin, short dental plates and occurs in the Wenlock (Bassett 1971, pl. 56, fig. 7a); (2) in a population of *Mesoleptostrophia filosa* from a siltstone overlying the Much Wenlock Limestone Formation a single specimen bears a pair of vestigial dental plates (Bassett 1971, pl 56, fig. 9a–b); (3) *Pembrostrophia* of Wenlock age possesses variably developed dental plates, but Harper and Boucot (1978, p. 156) regarded them as simply 'the basal part of the denticulate ridges'; (4) *Crinistrophia* and *Papillostrophia* of Emsian age which may have acquired short dental plates secondarily. Therefore the loss of dental plates, which progressed by simple shortening (rather than by a flaring towards, and subsequent merger with, the denticular plates and then the hinge line), may be considered an important trend in 'strophodontoid' evolutionary history (Williams 1953a; see also Text-fig. 18).

Cardinalia

The cardinalia of early strophomenoids from Llanvirn to Llandovery times were conservative in the different stocks, hence our reliance on this character for familial classification. However, in later stocks, chiefly the denticulate forms such as the Amphistrophiidae, Strophonellidae and Leptostrophiidae, but also in some stocks with smooth hinge lines such as the Glyptomenidae, Leptaeninae and the Rafinesquininae, the cardinalia evolved as described by Williams (1953a). In the earlier denticulate stocks, including *Eostropheodonta*, *Palaeoleptostrophia* and *Eostrophonella*, the cardinal process lobes were bladelike and antero-

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EXPLANATION OF PLATE 4

Figs 1–4. *Leptaena rugosa* Dalman; Dalmanitina Beds (Ashgill: Hirnantian), Ållebergsände, Västergötland, Sweden. 1–2, BB 67944; natural internal mould and latex cast, showing cardinalia of adult specimen; × 5. 3–4, BB 67946; natural internal mould and latex cast of the cardinalia of smaller specimen; × 5.

Figs 5–7. *Longvillia grandis* (J. de C. Sowerby); Marshbrook Beds (Caradoc: Marshbrookian), lane 60 m south of Marshbrook Quarry, Shropshire, England. 5, BB 30638; natural internal mould of dorsal valve; × 1. 6–7, enlargement of the cardinalia of the same specimen and latex cast; × 5.

Fig. 8. *Palaeoleptostrophia jamesoni* (Reed); Woodland Formation (Llandovery: Rhuddanian), Woodland Point, south of Girvan, Strathclyde, Scotland; BC 2471; latex cast of dorsal internal mould; × 8.

Fig. 9. *Rhytistrophia beckii* (Hall); Lower Helderberg Group (Lochkovian), Becraft's Mountain, Hudson, New York State, USA; AMNH 33167, syntype; latex cost of dorsal valve interior; × 6.

PLATE 4

RONG and COCKS, *Leptaena, Longvillia, Palaeoleptostrophia, Rhytistrophia*
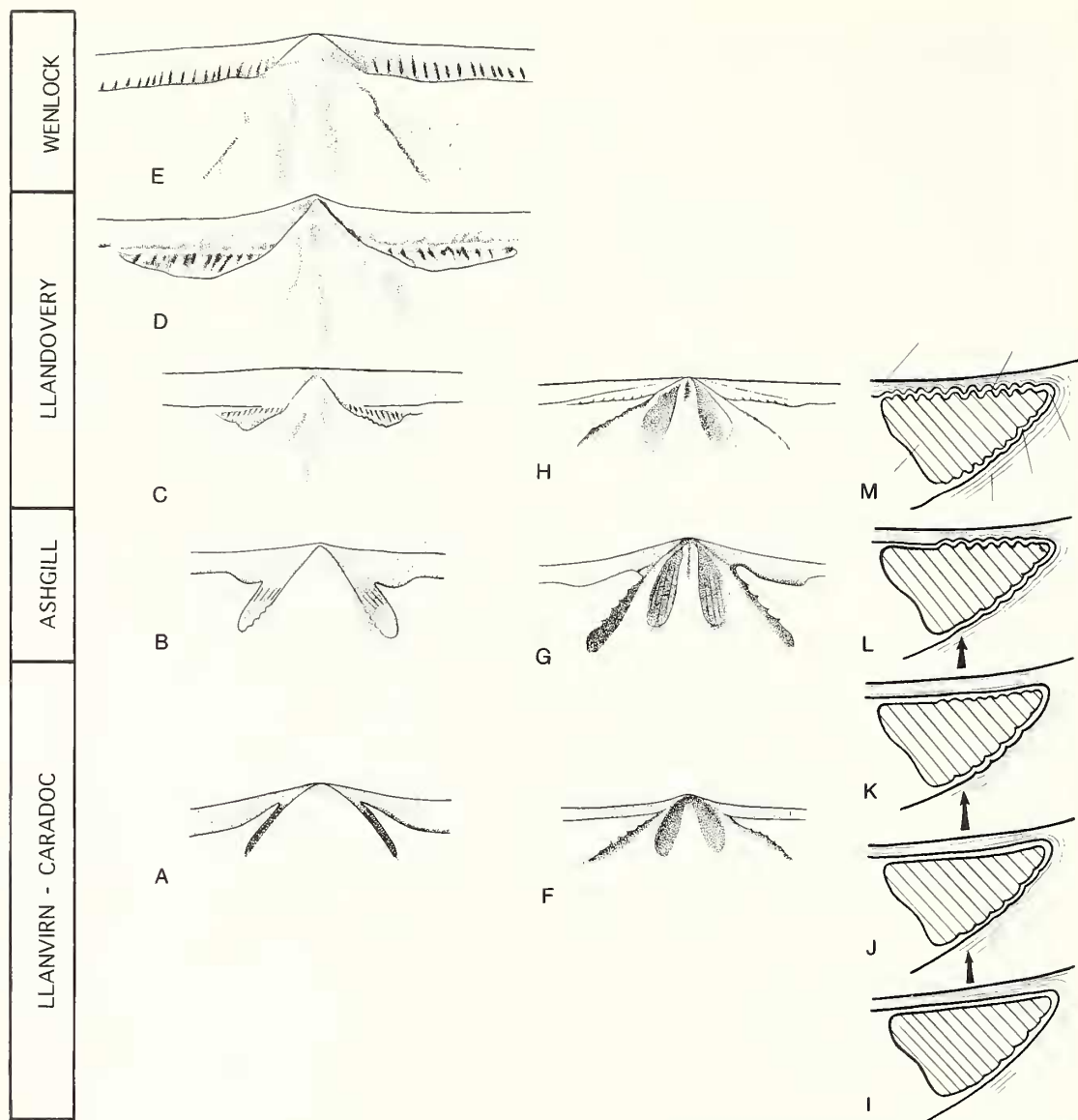
TEXT-FIG. 18. Evolution of articulation in the Strophomenoidea in late Ordovician and early Silurian. A–F, internal moulds. A, F, 'Macrocoelia'; B, G, Eostropheodonta; C, H, Palaeoleptostrophia; D, Brachyprion; E, Mesoleptostrophia filosa. I–M, schematic sections through strophomenoidean ventral hinge line, socket ridge and dental plate showing the development first of crenulations and subsequently denticles.

ventrally directed and situated between the pair of socket ridges which were generally stronger and more extensive than the later genera (Text-figs 18–19). The early stage was followed by one in which the cardinal process lobes became shorter and more swollen and progressively more ventrally directed, such as in Brachyprion, Eomegastrophia and Protomegastrophia. The stage is also seen in the late Llandovery leptaenine Mackerrovia. However, by middle Llandovery and Wenlock times, the first genera to show the final stage of
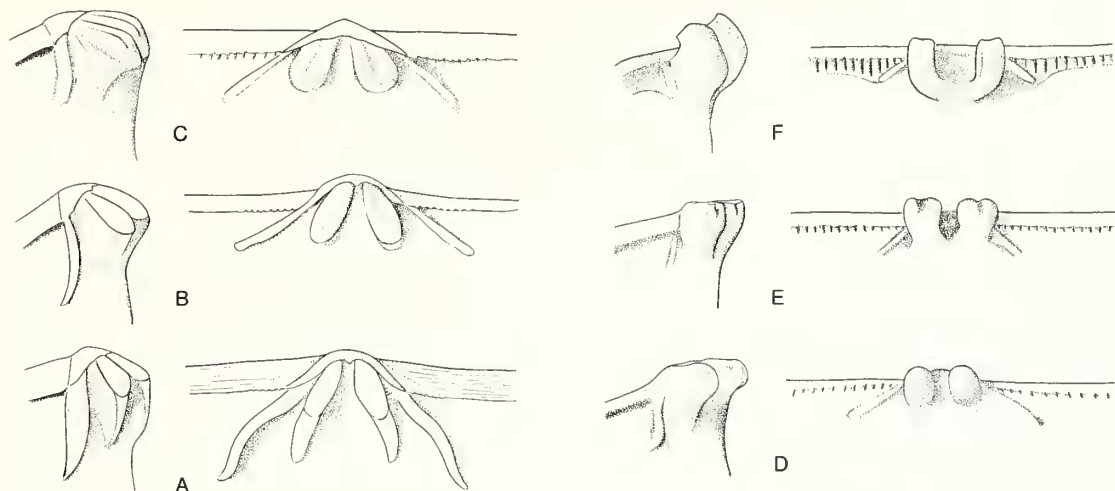
TEXT-FIG. 19. The development of cardinalia in the denticulate genera (with the exception of the Leptostrophiidae). A, *Eostrophonella*; B, *Brachyprion*; C, *Amphistrophia*; D, *Shaleria*; E, *Mesodouvillina*; F, *Strophonelloides*. No evolutionary succession from A to F is implied.

evolutionary development had evolved. These include the glyptomenids *Linostrophomena* and *Qianomena* from the middle and upper Llandovery of China respectively, and *Strophonella* (e.g. the well-known *S. euglypha* from the Much Wenlock Limestone Formation), in which the cardinal process lobes are posteroventrally directed (Text-fig. 19).

There is no known case of the reversal of this trend, that is from a posterior facing cardinal lobe ancestor giving rise to an antero-ventral facing descendant. The trend is also known outside the superfamily, within the Orthotetoidea and in some productoids. As the relative size of the cardinal process was also increasing, this was accompanied in many stocks by the spread and effectiveness of denticulation along the hinge line, leading firstly to the loss of dental plates in the ventral valve (see above) and subsequently to the reduction in size (such as in *Leptaenisca*, *Nadiastrophia* and *Sinostrophia*) and even loss of the socket ridges in the dorsal valve (such as in *Lissostrophia*, *Pholidostrophia*, *Protoleptostrophia* and *Rugoleptaena*). The position of the socket ridges also changed to be situated close to the cardinal process lobes. The timing of the change in direction of the cardinal process lobes differs in different stocks, although only a few members of the Leptaeninae and Leptostrophiidae, including *Leptaena* and *Leptostrophia* themselves (Pl. 7, fig. 6), are the only strophomenoids to display ventral-facing cardinal process lobes by Devonian times. Text-figure 20 shows the morphology of the cardinalia of eight genera within the Leptostrophiidae, ranging in age from the late Llandovery to Emsian, in which it can be seen that two separate later stocks evolved from the cardinalia morphology seen in *Mesoleptostrophia filosa*.

SYSTEMATIC NOTES

Genus STROPHOMENA de Blainville, 1824

Strophomena planumbona (Hall, 1847)

Plate 1, figures 1–7, 9–11; Text-figures 3, 8

1847   *Leptaena planumbona* Hall, p. 112, pl. 31B, figs 4a–e.
1850   *Strophomena* (*Leptaena*) *planumbona* (Hall) King, p. 103.
1892   *Strophomena planumbona* (Hall); Hall and Clarke, p. 249, pl. 9, figs 15–17; pl. 9A, figs 8–9.
non 1956   *Strophomena planumbona* (Hall); Cooper, p. 944, pl. 165, figs 1–2 [= *Strophomena vetusta* James].
1976   *Strophomena planumbona* (Hall); Pope, p. 154, figs 4:3, 5:1–3, 6:2, 7, 10–12.

Lectotype (here selected). AMNH 30247, conjoined valves, J. Hall collection, the original of Hall 1847, pl. 31B, fig. 4e, from the Trenton Limestone, Hudson River Group (Caradoc), Cincinnati, Ohio, USA (Pl. 1, figs 1–3, 5).

Discussion. Cocks (1990) reviewed the nomenclature of *Strophomena* and its type species. The genus was erected by de Blainville (1824) in a most peremptory manner, with its only listed species *Strophomena rugosa.* The true identity of *rugosa* has never been satisfactorily established, but there has been an assumption by many authors since the mid-nineteenth century that it is the same as *planumbona.* The position has been regularized finally by the ICZN (1992), which has determined that *planumbona* should be the type species of *Strophomena* and that the binomen *Strophomena rugosa* should be suppressed.

Opportunity is taken here to regularize the concept of *S. planumbona* by selecting a lectotype. Hall (1847, p. 112) mentioned the localities of Cincinnati and Oxford (Ohio), Madison (Indiana) and Maysville (Kentucky) all in 'a position equivalent to that of the Trenton Limestone'. Hall's illustrations of *planumbona* show three external views and one ventral valve interior. The only specimen in the Hall Collection which matches any of these illustrations is AMNH 30247, which has an identical convexity and outline as fig. 4e, and which we thus select as lectotype (Pl. 1, figs 1–3, 5). Some confusion also exists as to the true identity of the dorsal valve interior, which Hall (1847) did not illustrate. In the Hall Collection there is a box labelled *Strophomena planumbona* from Oxford, Ohio, in which there are several specimens, which belong to two separate species of *Strophomena.* Following Pope (1976) we determine one type as *S. planumbona* (Pl. 1, figs 7, 9) and the others as *S. vetusta* James (Pl. 1, fig. 8). However, James (1874) did not illustrate his species, and the difference between these two, as well as *S. filitexta* (Hall 1847) and a host of other North American late Ordovician nominal species of *Strophomena*, await further resolution and synonymy, preferably combined with a reappraisal of their relative stratigraphy based on fresh collections.

Genus LEPTAENA and its synonyns

Because *Leptaena*, with its rugosity and geniculation, is such a distinctive genus, a great number of species have been attributed to it since 1828. Many of these species have been promoted to be the types of new genera, but this has usually been done without a survey of related forms, and most workers (including ourselves) have been ignorant of the range of variation to be seen within the *Leptaena* group. Having checked many species assigned correctly to *Leptaena* we have found tremendous variation in shell shape, convexity, ornament, geniculation, the shape of the ventral

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EXPLANATION OF PLATE 5

Figs 1–2. *Brachyprion leda* (Billings); Jupiter Formation (Llandovery: Telychian), 3 km east of Jupiter River, Anticosti Island, Quebec, Canada; GSC 2442, lectotype slab. 1, internal mould of pedicle valve; ×8. 2, brachial valve interior; ×8.

Figs 3–4. *Eostrophonella eothen* Williams; Haverford Mudstone Formation (Llandovery: Rhuddanian), opposite entrance to gasworks, Haverfordwest, Dyfed, Wales; BC 50617. 3, latex cast of dorsal internal mould; ×1·5. 4, enlargement of the cardinalia of a latex cast of the same specimen also showing denticles on the posterior margins of the sockets; ×6.

Fig. 5. *Brachyprion* aff. *compressa* (J. de C. Sowerby); Lower Camregan Grits (Llandovery: Aeronian), Camregan Wood, east of Girvan, Strathclyde, Scotland; B 72901; latex cast of ventral internal mould, showing denticles on denticular plates and not on the hinge line; ×6.

Figs 6–7. *Eopholidostrophia sefinensis* (Williams); Rhydings Formation (Llandovery: Aeronian), Sefin footbridge, Llandovery, Dyfed, Wales; BB 95790; natural internal mould of dorsal valve and latex cast of it; ×4 and ×8.

PLATE 5

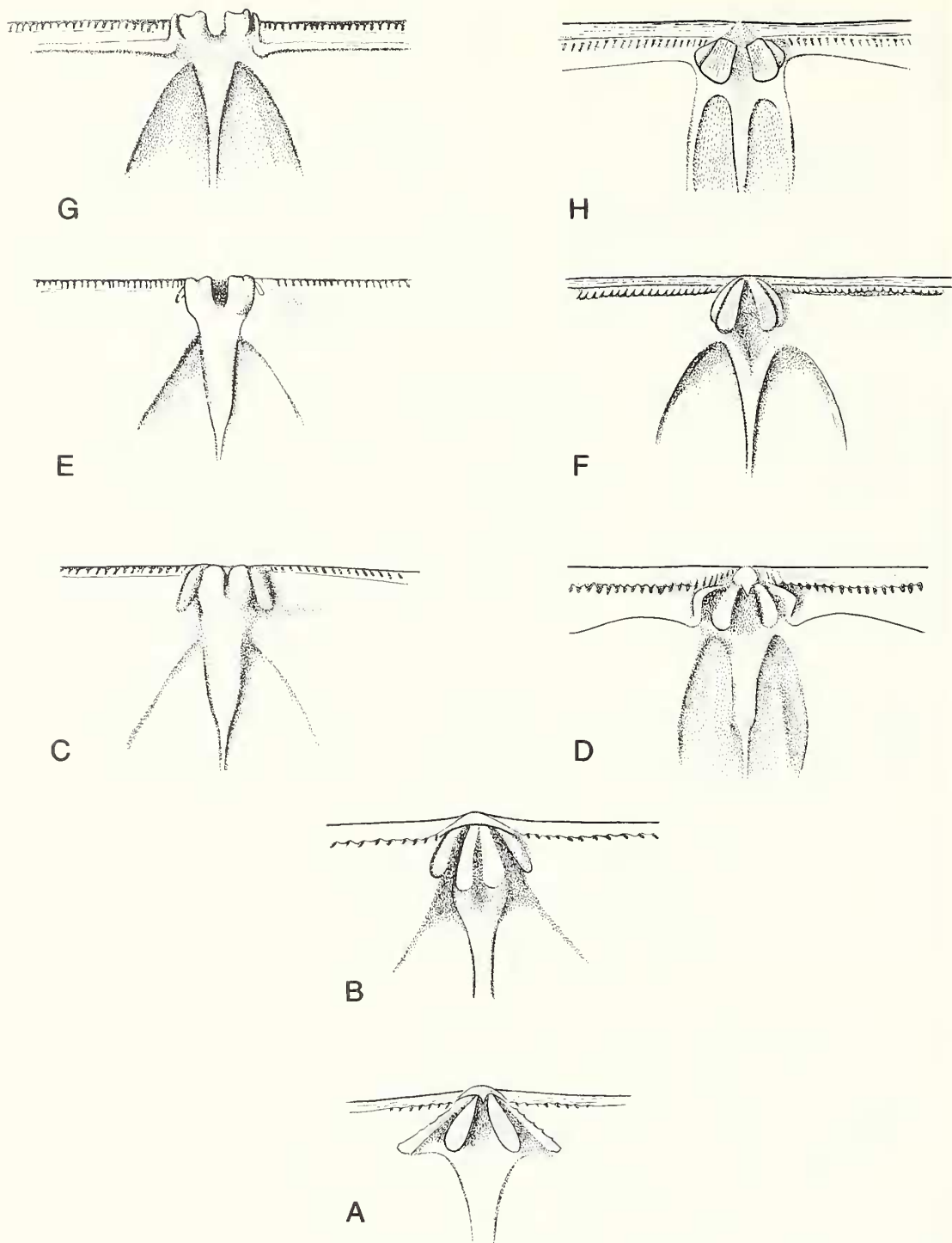
RONG and COCKS, *Brachyprion, Eostrophonella, Eopholidostrophia*
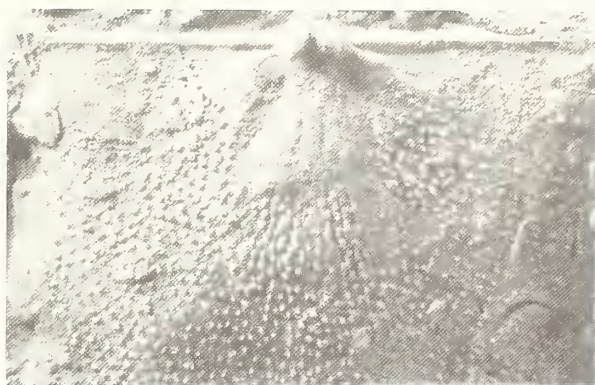
TEXT-FIG. 20. The development of cardinalia in the Leptostrophiidae. A, *Palaeoleptostrophia jamesoni*; B, *Mesoleptostrophia (Mesoleptostrophia) filosa*; C, *M. (M.) kartalensis*; D, *Leptostrophia (Rhytistrophia) beckii*; E, *Mesoleptostrophia (M.) explanata*; F, *Leptostrophia (Leptostrophia) magniventra*; G, *Mesoleptostrophia (Paraleptostrophia) clarkei*; H, *Leptostrophia (L.) magnifica*.
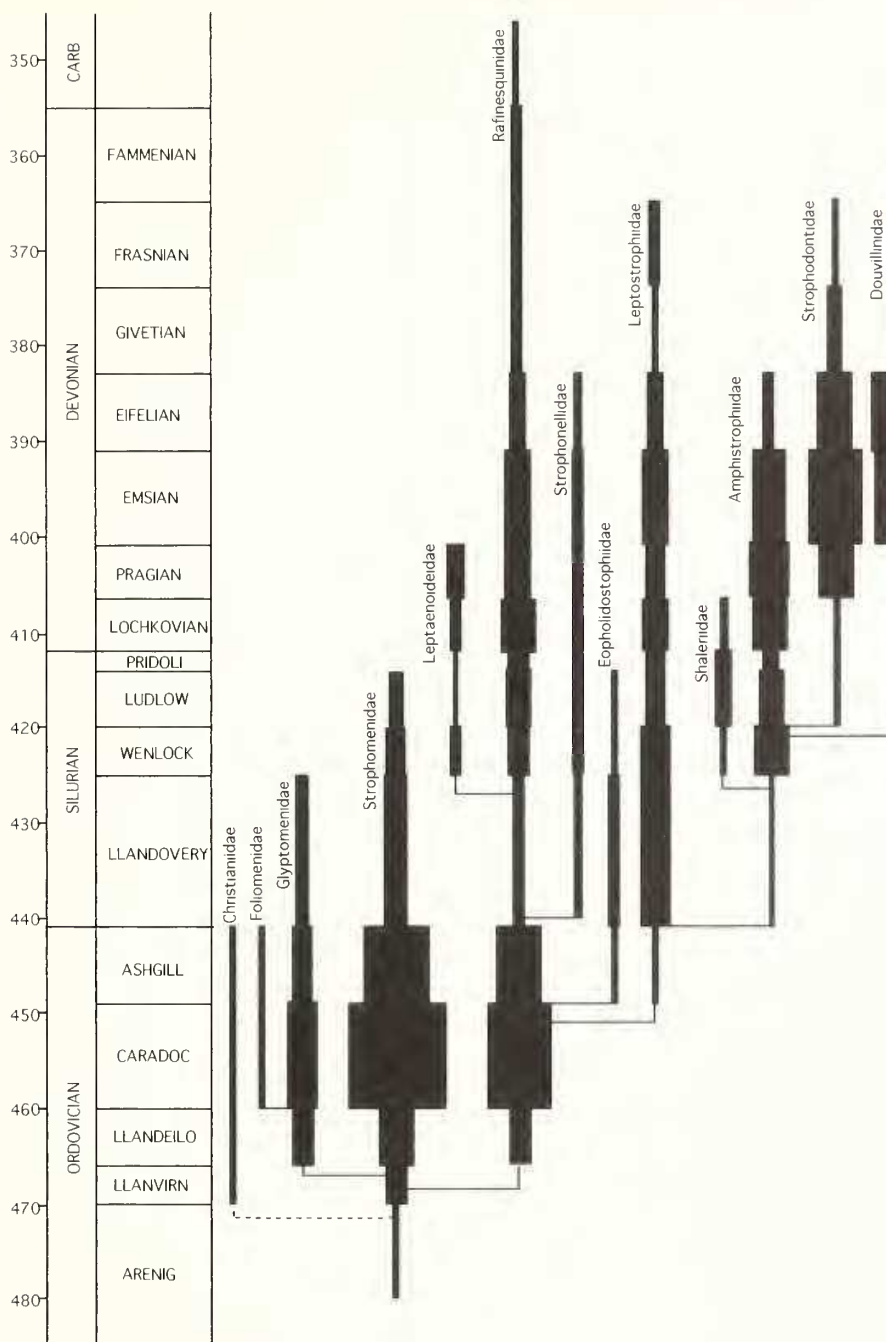
TEXT-FIG. 21. The stratigraphical ranges and postulated relationships of the families of the Strophomenoidea. Absolute ages in million years are shown on the left. The widths of the column representing each family indicates relative numbers of genera in each series (in the Ordovician and Silurian) or stage (in the Devonian).

muscle and the diaphragm and the trans-muscle ridges, sometimes within a single population. For example, within a sample of *L. trifidum* from Yichang, China, the trans-muscle ridges vary from absent to faint to reasonably strong (Rong 1984, p. 153). Similarly, the fine median ridge between the cardinal process lobes is variably present or absent in the same sample. These characters form the main basis of the erection of *Leptaenopoma* by Marek and Havlíček (1967) as separate from *Leptaena*, in addition to the 'blade-like brachiophores' present. As can be seen from our topotype *L. rugosa* material (Pl. 4, figs 3–4), the type species of *Leptaena*, the 'brachiophores' (which we term socket ridges) are also blade-like in young specimens, which is why we have placed the two genera in synonymy, following Mitchell (1977, p. 108). In a comparable way, Rõõmusoks (1989) erected seven new genera, apparently based on twelve different characters, but he did not compare them with other genera in the *Leptaena* group (apart from *Similoleptaena*, which he compared only with *Leptaena*). After our analysis we have been able to identify separately only one of his genera (*Septomena*) as a subgenus of *Leptaena* itself, based on the presence of strong trans-muscle ridges which appear to be stable across the population. The others we place into the synonymy of *Leptaena*, apart from *Estonomena* which we consider a synonym of *Kiaeromena*. *Kiaeromena* is itself closely related to *Leptaena*, differing only in its gentle rather than sharp geniculation. The characters which Rõõmusoks used to establish *Astamena*, *Kurnamena*, *Oandumena*, *Schmidtomena* and *Similoleptaena* we regard as being only of specific, rather than generic, importance. Similarly, Havlíček (*in* Havlíček and Štorch 1990) erected *Orhoria* because of the presence of slender socket ridges (which are again like those of young *Leptaena rugosa*, Pl. 4, figs 3–4) and by the lack of a peripheral rim inside the dorsal valve, which is a feature of youth in all leptaenines (the type species of *Orhoria* is small); hence again we synonymize *Orhoria* with *Leptaena*. The type species of *Leptaenella* Fredericks (*L. ventricosa* Hall and Clarke) has been assigned to *Leptaena* by Amsden (1963) for comparable reasons, and we follow him. The monotypic *Turgenostrophia* from the upper Silurian of Mongolia was established by Alekseeva *in* Alekseeva and Erlanger (1983) chiefly based on the absence of a dorsal valve diaphragm, but we consider that character varies substantially within the *Leptaena* group (in addition, her two figured specimens show only ventral valves), and again place the genus in synonymy. *Leptaenulopsis* is founded on small specimens (Williams 1965, p. H391), and the taxon is treated here as a *nomen dubium*.

Thus to summarize, *Astamena*, *Kurnamena*, *Leptaenella*, *Leptaenopoma*, *Oandumena*, *Orhoria*, *Schmidtomena*, *Similoleptaena*, and *Turgenostrophia* are all considered as synonyms of *Leptaena* (*Leptaena*), whilst *Leptaena* (*Septomena*) is considered a separate subgenus, and *Leptaenulopsis* a *nomen dubium*.

Genus BRACHYPRION Shaler, 1865

Brachyprion leda (Billings, 1860)

Plate 5, figures 1–2

1860   *Strophomena leda* Billings, p. 55, figs 2–3.
1865   *Brachyprion leda* (Billings) Shaler, p. 63.
1928   *Brachyprion leda* (Billings); Twenhofel, p. 188 [*pars*] ? pl. 22, figs 10–11.
1978   *Brachyprion* (*Brachyprion*) *leda* (Billings); Harper and Boucot, p. 15, pl. 36, figs 4, 6–7; ? fig. 5.

Lectotype (selected by Twenhofel 1928, p. 188), Geological Survey of Canada GSC 2442 from the Jupiter Formation (Telychian), 3·5 km east of Jupiter River, Anticosti Island, Quebec, Canada.

Discussion. The lectotype is a ventral valve only showing the exterior. It is fortunate, however, that the small slab bearing the lectotype (GSC 2442) includes not only three other ventral valve exteriors but also an excellent dorsal valve clearly showing the cardinalia (Pl. 5, fig. 2), and a ventral interior upon which details of the denticles and denticular plates may be seen (Pl. 5, fig. 1). These specimens resolve some doubts about the genus. In fact *B. leda* is rare within the Jupiter Formation (no specimens were found by one of us in two collecting visits to Anticosti Island) and it seems probable

that specimens of *Mesopholidostrophia* had also been included within it by some authors, including Twenhofel (1928). Harper and Boucot (1978) included *Protomegastrophia* and *Eomegastrophia* as subgenera of *Brachyprion*, but we regard the latter as a separate genus, because: (1) the dorsal valve of *Brachyprion* is much less convex than that of *Protomegastrophia* and *Eomegastrophia*; (2) *Brachyprion* has no dental plates and weak muscle bounding ridges within the ventral valve, in contrast to the better developed muscle bounding ridges of *Protomegastrophia* and the presence of dental plates within *Eomegastrophia*; (3) in *Brachyprion* the cardinal process lobes are shorter and less robust than in *Protomegastrophia*, and there is an alveolus present in *Protomegastrophia* which is absent or very poorly developed in *Brachyprion*; and (4) the ventral process is not well developed in *Brachyprion*. Within the dorsal interior of *B. leda* we have seen a small number of faint denticles on the posterior margins of the sockets. The Devonian species, such as *Megastrophia transitans* Johnson, listed under *Brachyprion* by Harper and Boucot (1978, p. 16) have a variety of different brachial valve internal structures – they are all rejected from the genus here.

Other species assigned to Brachyprion

Strophomena anticostiensis Shaler, 1865 (illustrated by Twenhofel 1928, pl. 22, figs 15–18) from the Gun River Formation (Aeronian) of Anticosti Island.
Orthis compressa J. de C. Sowerby, 1839 (revised by Cocks 1967, pl. 37, figs 1–7), from the Aeronian and Telychian of the Welsh Borderland.

Species questionably assigned to Brachyprion

Leptaena waltonii Davidson, 1848 (revised by Bassett 1971, p. 305, pl. 54, figs 1–5), from the Sheinwoodian of the Welsh Borderland (brachial interior unknown).
Strophomena dayi Davidson, 1871 (revised Bassett by 1974, p. 139, pl. 36, figs 11–14), from the Buildwas Formation (Sheinwoodian) of Shropshire (interiors unknown).

Genus PALAEOLEPTOSTROPHIA gen. nov.

Type species. Stropheodonta jamesoni Reed, 1917.

Diagnosis. Almost biplanate or very gently concavo-convex. Commonly unequally parvicostellate. Dental plates lacking. Denticles confined to small denticular plates in ventral valve, faint denticles may be present on posterior margins of the sockets in dorsal valve. Cardinal process lobes separated and located between socket ridges (like *Eostropheodonta*).

Discussion. The type species of *Palaeoleptostrophia* was assigned by Harper and Boucot (1978, p. 67) questionably to *Aphanomena* which is considered herein a subjective synonym of *Eostropheodonta* (see below). *Palaeoleptostrophia* resembles *Eostropheodonta* in shell shape, convexity and ornamentation, but it differs from the latter in the absence of dental plates and in the presence of denticles on the posterior margins of the sockets in the dorsal valve. The type species of *Mesoleptostrophia*, *M. kartalensis* from the Emsian of Turkey (Harper and Boucot 1978, p. 68, pl. 3, figs 2–3), is characterized by the distinctive cardinalia in which the cardinal process lobes are close together and converge at their bases on to a median ridge. The socket ridges of *M. kartalensis* are very short and truncated (Text-fig. 20c) and the ventral valve process is well developed, in contrast to *P. jamesoni* in which the ventral process is hardly developed. The well-known late Wenlock to mid-Ludlow species *filosa* was assigned to *Leptostrophiella* by Harper and Boucot

(1978, p. 75), but we regard this species as the earliest representative of *Mesoleptostrophia* (Text-fig. 20B). It is probable that *Palaeoleptostrophia* is the ancestor of *Mesoleptostrophia*, and the point of change is when the denticles migrated on to the hinge line and this coincided with the convergence of the cardinal process lobes on to a median ridge and with the acquisition of the stronger ventral process.

The genus *Castellaroina* occurs in poorly dated, but probably Wenlock or Ludlow age beds in South America. This appears to have a stronger ventral process than *Palaeoleptostrophia*. Examination of the type material of *C. fascifer* (Kayser) reveals that the genus lacks dental plates and is a close relative of both *Brachyprion* and *Palaeoleptostrophia*. It differs from *Brachyprion* in arrangement of the socket ridges and in possessing a stronger and longer cardinal process. *Castellaroina* differs from *Palaeoleptostrophia* in its less well-developed socket ridges and in a stronger and longer cardinal process, and it also possesses a pair of additional enigmatic ridges fused with the hinge line and posterior to the socket ridges.

Palaeoleptostrophia differs from *Brachyprion* in being less convex in its ventral valve, is thinner-shelled, has a stronger notothyrium and thinner but more erect socket ridges, and the anterior parts of its cardinal process lobes converge slightly on to the broad median ridge (Pl. 4, fig. 8). We do not know if *Brachyprion* evolved directly from *Palaeoleptostrophia* or whether the two genera were derived independently from *Eostropheodonta*.

Species assigned

Stropheodonta jamesoni Reed, 1917, from the Rhuddanian of Girvan, Scotland.
Leptostrophia tenuis Williams, 1951, from the Aeronian of the type Llandovery area, Wales.
Leptostrophia ostrina Cocks, 1967, from the Telychian of the Welsh Borderland.

Species possibly assigned

Aphanomena sp. of Harper and Boucot 1978, pl. 1, fig. 2, from the Aeronian of Quebec (ventral valve not known).

<center>

Palaeoleptostrophia jamesoni (Reed, 1917)

Plate 4, figure 8; Plate 6, figures 1–5; Text-figures 18, 20, 22

</center>

1883   *Strophomena corrugatella* Davidson [*pars*], p. 192, pl. 15, fig. 25; *non* figs 23–24, 26.

<center>EXPLANATION OF PLATE 6</center>

Figs 1–5. *Palaeoleptostrophia jamesoni* (Reed); Woodland Formation (Llandovery: Rhuddanian), Woodland Point, south of Girvan, Strathclyde, Scotland. 1–2, BC 2471; latex cast and natural internal mould of a dorsal valve; × 1·5. 3–5, BC 2454; natural internal mould of a ventral valve and ventral and anterior enlargements of a latex cast of it showing denticles on denticular plates and on the antero-median parts of the teeth; 3, × 1·5, 4–5, × 8.

Figs 6, 10. *Douvillinaria variabilis* (Calvin); Independence Formation (Frasnian), Middle Amana, Iowa, USA. 6, BB 57970; dorsal interior; × 6. 10, BB 57971; posterior view of conjoined valves showing the narrow and convex deltidium and chilidium; × 8.

Figs 7–9, 11–12. *Strophonelloides reversa* (Hall); Cerro Gordo Member, Hackberry Formation (Frasnian), Rockford, Iowa, USA. 7–9, B 41635; lateral, dorsal and posterior views of a dorsal valve, the latter showing crenulations on the socket ridges; 7–8, × 2, 9, × 6. 11–12, BC 13412; ventral and anterior views of ventral valve, showing the distinctive ventral process; 11, × 2, 12, × 4.

PLATE 6

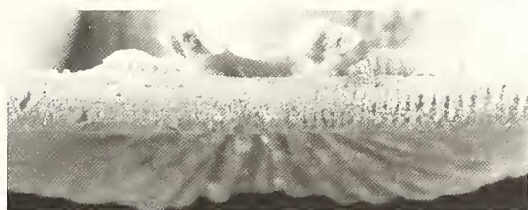
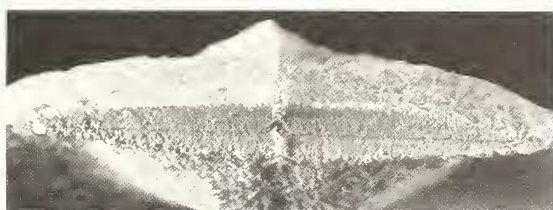RONG and COCKS, *Palaeoleptostrophia, Douvillinaria, Strophonelloides*

1917   *Stropheodonta jamesoni* Reed, p. 893, pl. 16, figs 28–30; pl. 17, figs 1–2.
?1949   *Eostropheodonta reedi* Bancroft, p. 10, pl. 2, fig. 9.
?1951   *Leptostrophia tenuis antecedens* Williams, p. 125, pl. 8, figs 5–6.
1978   *Leptostrophia jamesoni* (Reed) Cocks, p. 127.
?1987   *Leptostrophia antecedens* Williams; Temple, p. 84, pl. 9, figs 10–12.

Lectotype. Selected by Cocks 1978, p. 127, B73036, conjoined valves, the original of Reed 1917, pl. 16, fig. 29, from Woodland Formation (Rhuddanian), Woodland Point, near Girvan, Scotland.

Discussion. Cocks (1978) synonymized *reedi* and *antecedens*, although Temple (1987) preferred to regard *reedi* as a *nomen dubium* and used *antecedens*. Both come from the Haverford Mudstone Formation of Rhuddanian age from Wales. *P. jamesoni* is of the same Ruddanian age and is well represented by more than a hundred specimens in the Gray Collection from the Woodland Formation of Girvan. It is probably a senior synonym of *reedi/antecedens*, but is left in queried synonymy until the Woodland Point fauna is fully revised.

Genus EOSTROPHEODONTA Bancroft, 1949

1949   *Eostropheodonta* Bancroft, p. 9.
1951   *Stropheodonta* (*Eostropheodonta*) Bancroft; Williams, p. 123.
1965   *Eostropheodonta* Bancroft; Temple, p. 410.
1967   *Leptostrophia* (*Eostropheodonta*) Bancroft; Cocks, p. 253.
1967   *Eostropheodonta* Bancroft; Havlíček, p. 81.
1968   *Aphanomena* Bergström, p. 13.
1968   *Leptostrophia* (*Eostropheodonta*) Williams; Bergström, p. 17.
1971   *Leptostrophia* (*Eostropheodonta*) Bancroft; Bassett, p. 318.
1972   *Eoleptostrophia* Boucot *in* Amos, p. 11.
1974   *Rafinesquina*? Hall and Clarke; Amsden, p. 52.
1978   *Eostropheodonta* Bancroft; Cocks, p. 125.
1978   *Eostropheodonta* Lamont; Harper and Boucot, p. 102 [*pars*].
1978   *Aphanomena* Bergström; Harper and Boucot, p. 66 [*pars*].
1984   *Aphanomena* Bergström; Rong, p. 156.
?1985   *Hibernodonta* Harper *et al.*, p. 300.

Discussion. In the upper Ordovician, strophomenoid brachiopods are very common and widespread at many localities, particularly in the uppermost Ashgill *Hirnantia* Fauna. They have attracted the attention of many systematists for more than a hundred years and, as a result, many taxonomic names have been erected for them. As with all other strophomenoids dealt with in this paper, we have looked firstly at the cardinalia, secondly at the presence and positioning of any denticles present, and lastly at other aspects of the morphology such as shape and ornament. The oldest established genus in this group is *Eostropheodonta*, whose type species is *E. hirnantensis* from the uppermost Ashgill of Wales, which was revised comprehensively by Temple (1965). The cardinal process lobes are of Type B, and dental plates are present. There are approximately four to six denticles present on each of a pair of denticular plates; these denticular plates (Williams 1951, p. 122, fig. 22) are the dorsal surface of the teeth, and extend for only a very short distance along the hinge line. On the antero-median facets of the teeth (Text-figs 8, 18) there are also crenulations, which do not usually correspond in number to the denticles. Sometimes an individual denticle continues round the corner of the tooth to be continuous with a crenulation, but this is not always the case. In the dorsal valve there are no denticles on the hinge line (posterior margins of the sockets), but there are crenulations of the posterior faces of the socket ridges which interlock into most, but not all, of the crenulations of the ventral valve.

The ornamentation is variable. In the topotype population of *E. hirnantensis* three types of ornament occur; unequally parvicostellate (Temple 1965, pl. 17, fig. 6), evenly multicostellate (Temple 1965, p. 411) and fascicostellate (Temple 1965, pl. 18, fig. 7), and all variations between these combinations may be found in the Natural History Museum collections. Later authors have
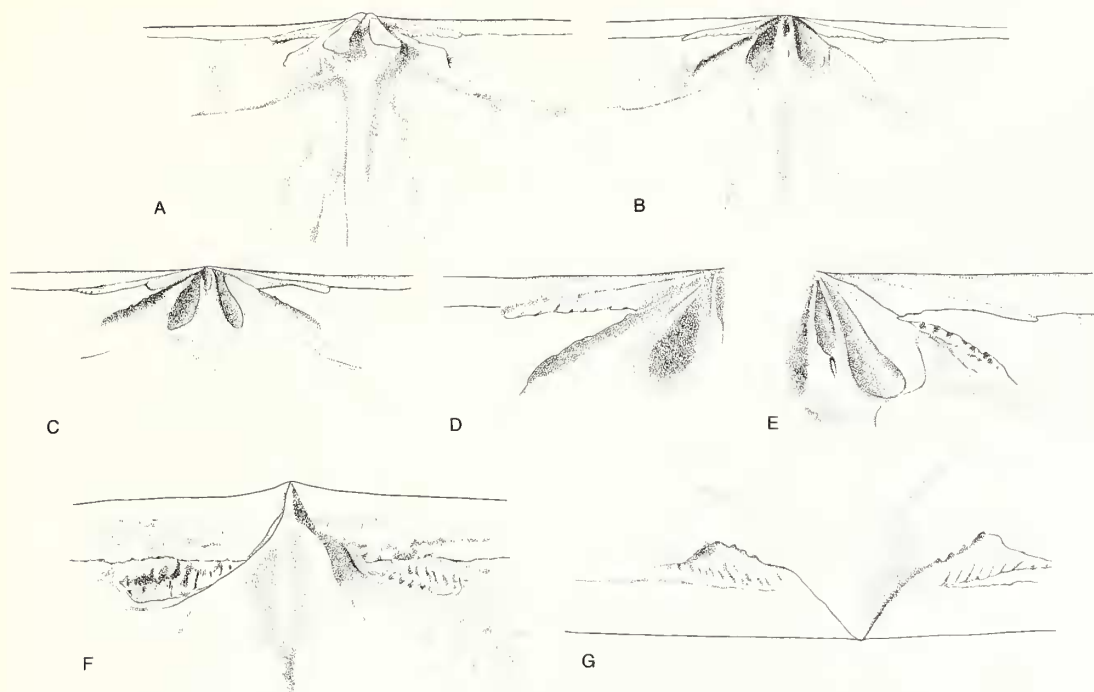
TEXT-FIG. 22. The articulation and cardinalia of *Palaeoleptostrophia jamesoni*. A–B, D–E, BC 2471; dorsal internal mould and latex cast showing denticles on the posterior margin of the sockets and on the anterior facets of the socket ridges, ×6 and ×12 respectively; C, BC 2472; a natural internal mould; ×6; F–G, BC 2454; ventral valve; showing denticules on the denticular plates and viewed ventrally and posteriorly, all from the topotype population from the Woodland Formation (Llandovery: Rhuddanian) at Woodland Point, Girvan, Scotland; ×12.

unfortunately placed undue significance on aspects of the ribbing, for example in Harper and Boucot (1978, p. 101) in the redefinition of the Eostropheodontidae. When Bergström (1968, p. 13) established *Aphanomena* he did not compare it with *Eostropheodonta*, and Harper and Boucot (1978, p. 66) separated the two genera only by the allegedly different ornamentation (parvicostellate in *Aphanomena*, and fascicostellate in *Eostropheodonta*). Boucot *in* Amos (1972) established *Eoleptostrophia* with type species *E. mullochensis*, on the basis of its 'evenly parvicostellate' ornament; after examination of extensive topotype collections, we also assign this species to *Eostropheodonta*.

We have re-examined the type specimens of *Hibernodonta praeco*, BC9195–7, which was established by Harper *et al*. (1985, p. 301), who described the 'hinge line denticulate along at least three-quarters of width'. On the contrary, there are no denticles on the hinge line, although in the ventral valve there are some very weak and poorly defined low denticles on the denticular plates. There are, however, six or seven much stronger crenulations on the antero-median facets of the teeth, and corresponding crenulations on the posterior faces of the socket ridges in the dorsal valve. Thus we consider *Hibernodonta* to be within the generic concept of *Eostropheodonta*, but retain it as a separate subgenus from *E.* (*Eostropheodonta*) because the denticles on the denticular plates are scarcely developed. The age of *Hibernodonta* and the Clashford House Formation in which it occurs is not established definitively, but it has been provisionally assigned to the late Caradoc (Harper *et al*. 1985, p. 289), and thus provides an interesting link between *Eostropheodonta* and its rafinesquinid ancestors. The cardinalia of *Hibernodonta* are very similar to *Hedstroemina*, in which

crenulations are found, and also to *Kjaerina* (Pl. 3, figs 1–5), although we have seen no crenulations in the latter genus. We also assign *Brachyprion stropheodontoides* Savage to *Eostropheodonta*. Amsden (1974, p. 52) revised this species and assigned it to *Rafinesquina?*, but he illustrated denticles on denticular plates (1974, pl. 12, fig. 2*i*), which are distributed in the same way as in *Eostropheodonta hirnantensis*. Thus the distribution of the genus ranges from upper Caradoc to lower Wenlock (the *Leptostrophia* (*Eostropheodonta*) sp. of Bassett 1971, pl. 56, figs 7–8) and it occurs over most of the world, with its acme in the *Hirnantia* Fauna of the upper Ashgill.

Genera BOUCOTSTROPHIA, LEPTOSTROPHIELLA, MESOLEPTOSTROPHIA *and* RHENOSTROPHIA

In 1960, Boucot erected *Rhenostrophia* with *Orthis subarachnoidea* d'Archiac and Verneuil as type species. As Jahnke (1971, p. 59) pointed out, there is only one type specimen of *R. subarachnoidea*, which is merely the exterior of a ventral valve, and the genus is therefore best considered as a *nomen dubium* until the type species is properly redescribed from new topotype collections. Jahnke (1971, p. 59) also pointed out that *subarachnoidea* might be conspecific with *Orthis explanata* Sowerby, which is the type species of *Leptostrophiella* Harper and Boucot (1978, p. 74). García-Alcade (1992, p. 66) accepted Jahnke's conclusion, but unfortunately suggested rejection of *Rhenostrophia* in favour of *Leptostrophiella*, which is not allowable under the ICZN rules of priority. After revision, we consider that *Leptostrophiella* is a subjective synonym of *Mesoleptostrophia* Harper and Boucot (1978, p. 68), whose type species, *M. kartalensis* Harper and Boucot comes from the Emsian of Turkey. A further genus, *Boucotstrophia* Jahnke (1981, p. 150), whose type species (*Stropheodonta herculea* Drevermann from the Pragian of Germany) was assigned to *Rhenostrophia* by Harper and Boucot (1978, p. 173).

Since *R. subarachnoidea* has not yet been revised, we are faced with a dilemma. There are at least two separate forms which are firstly, a leptostrophiid, which includes the species *explanata* and *kartalensis*, and secondly, a strophodontid, which includes the species *herculea*. We propose to use *Mesoleptostrophia* for the first form and *Boucotstrophia* for the second form, and treat *subarachnoidea* and its associated genus *Rhenostrophia* as a *nomen dubium*. If *Rhenostrophia* is ever revised and resurrected, then it will probably be a senior synonym of *Mesoleptostrophia*, or less probably *Boucotstrophia*, but we recommend its non-usage.

Family PHOLIDOSTROPHIIDAE Stainbrook, 1943

Stanbrook (1943) erected the subfamily Pholidostrophiinae because of a perceived link between the strophodontids and chonetoids. This was not at first followed by Williams (1953*a*, 1953*b*), who included the group within the Strophoedontinae; but Williams (1965) later defined the subfamily to include *Pholidostrophia* (and its subgenus *Mesopholidostrophia*) and *Lissostrophia* (with its subgenus

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EXPLANATION OF PLATE 7

Figs 1–3. *Megastrophia concava* (Hall); Silica Shales, Traverse Group (Eifelian–Givetian), Sylvania, Ohio, USA; BB 16709; postero-ventral, posterior and ventral views of ventral valve showing crenulations on the socket ridges; 1–2, × 6, 3, × 2.

Fig. 4. *Protodouvillina inaequistriata* (Conrad); Hamilton Group (Eifelian–Givetian), Bristol and Canandagua Lake, New York State, USA; AMNH 37217; enlargement of the posterior part of the dorsal interior; × 6.

Fig. 5. *Strophodonta demissa* (Conrad); Upper Ferron Point Formation (Givetian), Alpena, Michigan, USA; BB 16568; enlargement of the cardinalia; × 6.

Fig. 6. *Leptostrophia magnifica* (Hall); Oriskany Sandstone (Pragian), Schoharie, New York State, USA; BC 13063; postero-dorsal view of latex cast of cardinalia; × 3.

Fig. 7. *Amphistrophia* (*Amphistrophiella*) *funiculata* (M'Coy); Mulde Marl (Wenlock; Homerian), Däpps, Gotland, Sweden; BC 4363; enlargement of cardinialia; × 6.
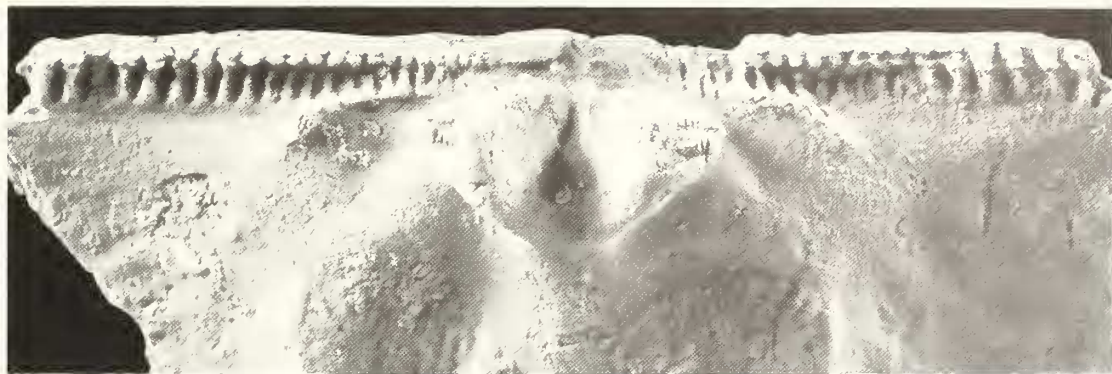
PLATE 7

RONG and COCKS, strophomenoid brachiopods

Mesolissostrophia). Sokolskaya (1960, p. 215) elevated the subfamily to familial rank. A substantial contribution by Harper *et al.* (1967) followed, in which the subfamily included *Ancylostrophia*, *Eopholidostrophia*, *Nadiastrophia*, *Pholidostrophia* (and its subgenus *Mesopholidostrophia*), *Phragmostrophia*, *Radiomena*, *Teichostrophia*, and *Telaeoshaleria*, but not *Lissostrophia*, although they synonymized *Mesolissostrophia* with *Mesopholidostrophia* since their type species were deemed conspecific. In their subsequent revision, Harper and Boucot (1978) considered the Pholidostrophiidae as of familial rank, with the subfamilies Pholidostrophiinae and Teichostrophiinae, and erected the Lissostrophiidae to include *Lissostrophia* alone, although they had removed *Nadiastrophia* to the Douvillinidae and erected a further new family for *Telaeoshaleria*. We have reviewed all these genera in relationship to all other unrelated genera and have come to the conclusion that there is no validity in the previously published concept of the family or subfamily erected around *Pholidostrophia*. The genera can be grouped elsewhere as follows: (1) *Pholidostrophia*, *Lissostrophia* and *Parapholidostrophia* are placed with the Strophodontidae, based on the distinctive shapes of the ventral valve muscle field and also the trans-muscle ridges, central median septum and side septa in the dorsal valve. Thus we consider the family and subfamily name to be a junior synonym of Strophodontidae Caster, 1939; (2) *Eopholidostrophia* and *Mesopholidostrophia* are placed in the Eopholidostrophiidae fam. nov. (see below); (3) *Nadiastrophia*, *Phragmostrophia*, *Radiomena*, *Teichostrophia* (and its synonym *Ancylostrophia*), and *Telaeoshaleria* are placed within the Douvillinidae, also based on the ventral muscle field and dorsal internal structures.

One reason why *Pholidostrophia* and *Mesopholidostrophia* have been considered related in the past has been because of their notable nacreous shells, the only ones in the entire Strophomenoidea; however that shell condition is seen developed polyphyletically elsewhere in the Brachiopoda and in the Mollusca, Bryozoa, and other phyla.

Family EOPHOLIDOSTROPHIIDAE fam. nov.

Diagnosis. Denticles on hinge line or denticular plates. Moderately to strongly concavo-convex. Triangular ventral valve muscle field very weakly impressed, open anteriorly and with no muscle bounding ridges except for a short distance posterolaterally. No radial ridges within the ventral muscle field, unlike the Leptostrophiidae. Cardinal process lobes small, separate and ventrally directed. Short thin socket ridges. Side septa absent.

Type genus. *Eopholidostrophia* Harper *et al.* 1967.

Included genera. *Eopholidostrophia*, *Origostrophia* Mitchell, 1977, and *Mesopholidostrophia* Williams, 1950 (with its junior synonym *Mesolissostrophia* Williams, 1950). Range: Ashgill (Rawtheyan) to Ludlow (Gorstian).

Discussion. Although *Eopholidostrophia* is similar to early leptostrophiids in its muscle field shape and cardinalia, the gross differences in shell-shape and covexity between it and *Eostropheodonta* and its relatives indicate that they were derived from different stocks within the Rafinesquininae, and thus *Eopholidostrophia* and *Eostropheodonta* should be assigned to separate families to prevent the Leptostrophiidae from becoming a polyphyletic taxon. The strong dental plates of *Eostropheodonta* are absent in *Eopholidostrophia*. The Ashgill species *Eopholidostrophia matutinum* and *E. fragilis* have more flaring and narrower denticular plates than contemporary *Eostropheodonta*, such as the widespread *E. hirnantensis* (Text-fig. 18), and thus the denticulation of *Eopholidostrophia* progressed along the standard evolutionary path separately from *Eostropheodonta* and its descendants *Palaeoleptostrophia* and *Brachyprion*.

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APPENDIX

Strophomenoids with crenulated teeth and sockets

In this list the following symbols are used: ∗, we have seen the specimens; crenulations have been reported or observed in ⊙ the ventral valve, ○ the dorsal valve and ● both valves.

In the **Strophomenidae** we have seen crenulations in (1) ● *Strophomena planumbona* (Hall), the type species of *Strophomena* (Spjeldnaes 1957, fig. 3E–G, and ∗AMNH 30248; Plate 1, figs 10–11); (2) ⊙ *S. bilix* (Lamont) [syn. *S. cancellata* (Portlock)] (Mitchell 1977, p. 98); (3) ○ *S. filitexta* (Hall) (∗AMNH 918/5(*a*); Plate 1, fig. 8); (4) ⊙ *S. neglecta* (James) (Spjeldnaes 1957, pl. 12, fig. 8); (5) ● *S. satterfieldi* Amsden (1974, p. 51, pl. 23, fig. 2*a–b*); (6) ● *Bellinurina tenuicorrugata* (Reed) (Williams 1962, p. 205); (7) ● *Biparetis paucirugosus* Amsden (1974, pl. 21, fig. 1*c*, *p–q*; pl. 22, fig. 1*b*); (8) *Drumnuckina donax* (Reed) (∗B7290); (9) ⊙ *Furcitella plicata* Cooper (∗USNM 117751*a*); (10) ○ *Iberomena sardoa* (Vinassa) (Villas 1985, pl. 22, fig. 8; Havlíček *et al.* 1987, pl. 9, fig. 13); (11) ⊙ *Infurca tessellata* Percival (1979, p. 185, pl. 2, figs 14–15); (12) ● *Katastrophomena woodlandensis* (Reed) (∗BC2170; Plate 1, fig. 12); (13) ⊙ *Longvillia grandis* (J. de C. Sowerby) (∗B8528); (14) ⊙ *Luhaia vardi roomusoksi* Sheehan (1987, p. 40); (15) ○ *Maakina kulinnensis* Andreeva (*in* Nikiforova and Andreeva 1961, pl. 33, figs 5, 7) [this species has strong denticles in the anterior face of the sockets]; (16) ● *Macrocoelia stenomuscula* Laurie (1991, p. 72, fig. 41B); (17) ● *Oepikina septata* Salmon, the type species of *Oepikina* (USNM 117829*c*; Plate 2, fig. 8; Plate 3, figs 6–7); (18) ⊙ *Oepikina speciosa* Cooper (1956, pl. 249, fig. 7); (19) ○ *Oepikina? walliensis* Percival (1991, p. 149) [the cardinalia of this species is of the *Strophomena* group]; (20) ⊙ *Pseudostrophomena reclinis* Rõõmusoks (∗BB91296); (21) ⊙ *Rhipidomena tennesseensis* (Willard) (Cooper 1956, pl. 253, figs 12–13); (22) ● *Trigrammaria ampla* Percival (1991, p. 149, fig. 15–4); (23) ⊙ *Trigrammaria virve* Rõõmusoks (1985, p. 134).

In the **Rafinesquinidae** we have observed crenulations in both subfamilies; in the **Rafinesquininae**: (1) ○ *Rafinesquina alternata* (Hall), the type species of *Rafinesquina* (∗B39912); (2) ○ *Hedstroemina fragilis* (Bancroft) (∗BB73550); (3) ○ *Hedstroemina* sp. (Bergström 1968, p. 13); (4) ○ '*Macrocoelia' llandeiloensis elongata* Lockley and Williams (∗BB92421) [this species should be assigned to the rafinesquinids, but *Macrocoelia* is a strophomenid]. In the **Leptaeninae**: (1) ○ *Leptaena contermina* Cocks (1968, p. 6, fig. 10); (2) ○ *L. depressa* (J. de C. Sowerby; Havlíček 1967, pl. 16, fig. 16; ∗B43366 and others; (3) ○ *Leptaena minuta* Kiaer (Mitchell 1977, p. 106, pl. 23, fig. 10); (4) ○ *L.* cf. *ordovicica* Cooper (Williams 1962, p. 198); (5) ● *L. reedi* Cocks (Temple 1970, p. 46); (6) ○ *Leptaena rugosa* Dalman, the type species of *Leptaena* (Bergström 1968, p. 15; Mitchell 1977, p. 109, pl. 23, figs 16–17, 25–26); (7) ○ *Leptaenopoma trifidum* Marek and Havlíček (Bergström 1968, p. 16, text-fig. 8); (8) ● *L. valentia* Cocks (Temple 1970, pl. 44); (9) ○ *Leptaena ventricosa* Williams (1963, p. 462; with sockets striated); (10) ○ *Kosomena kosia* Havlíček (*in* Havlíček and Štorch 1990, p. 71); (11) *Leptagonia analoga* (Williams 1965, p. H394); (12) *Mackerrovia lobatus* (Lamont and Gilbert) (∗BC50573).

In the **Glyptomenidae** there are crenulations in: (1) ● *Mjoesina moorei* Mitchell (1977, p. 102, pl. 21, figs 11, 13, 16); (2) ○ *M. rugata*; and (3) ○ *M. rugata plana* Williams (1962, p. 208). In the **Leptaenoideidae**: (1) ● *Liljevallia amorpha* Zhang (1989, p. 107, pl. 5, figs 13, 15–17); (2) ⊙ *Leptaenisca concava* Hall (Yale Peabody Museum 28115); (3) *Leptaenomendax chaconae* Gracia-Alcade (1978, p. 256).